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Fire Regimes and Ecosystem Properties

Proceedings of the Conference

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PROCEEDINGS OF THE CONFERENCE

FIRE REGIMES AND ECOSYSTEM PROPERTIES



December 11-15, 1978

Honolulu, Hawaii

Technical coordinators:

H. A. Mooney

Professor of Biological Sciences, Department of Biological Sciences, Stanford University, Stanford, California

T.M. Bonnicksen

Assistant Professor of Forestry, Department of Forestry, University of Wisconsin, Madison, Wisconsin

N. L. Christensen

Associate Professor of Botany, Duke University, Durham, North Carolina

J. E. Lotan

Program Manager, Fire Effects Research and Development Program, Intermountain Forest and Range Experiment Station, USDA Forest Service, Missoula, Montana

W. A. Reiners

Professor of Biological Sciences, Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire

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FOREWORD

This volume is one of a series of contributions from different countries to an international "project" on the ecological effects of fire. Its appearance is opportune for it comes at a time of remarkable change in attitudes to fire on the part of ecologists and land managers. Fire is perhaps the most ancient tool by which man has exerted a widespread influence on vegetation, but not unnaturally the destructive effects of uncontrolled fire have been greatly feared and much effort has been devoted to fire prevention. Recently, however, there has been increasing realization that natural, lightning-induced fire has been, in many parts of the world, a recurrent influence in the development of the vegetation, and that man may store up trouble for himself by its elimination.

Unfortunately, though not unnaturally, the subject is one which has aroused deep-seated emotions and controversy. There is a considerable literature devoted to it, but this has been permeated with special pleading both from those who for the best of reasons have invested much in fire prevention and from those who see the use of fire in vegetation management almost as a panacea for all ills. It is the purpose of this volume to assemble the factual results of research on this topic and to consider their application to practical problems, thereby (it is hoped) contributing to a more balanced view.

Recent research has, in fact, revealed a great deal of the utmost interest and significance, for example on the past frequency and distribution of natural fires in forest, scrub, and grassland regions, and on the role of man in changing the incidence of fire. It has given exciting new insights on the part played by fire in ecosystem functioning and as an agent of natural selection, leading to the evolution of adaptive characters in species which are to some degree resistant to fire. New ideas have arisen on the nature of the successional changes following burning. These, together with their implications for management, both in regard to production and wildlife conservation, are among the important subjects treated in this book.

C. H. Gimingham
Duke University
Old Aberdeen

PREFACE

The proceedings of this meeting represent an attempt to synthesize our knowledge of the ecological impact of fire frequency and intensity on species characteristics and ecosystem function, with the express purpose of examining this information for possible utilization in landscape management.

In the United States there has been a long history of a diversity of viewpoints, quite often strongly polarized, on the most appropriate management policy for a given natural ecosystem type, particularly in relation to fire. It can be argued that as our detailed knowledge increases on how particular species types and ecosystems respond to given perturbations, these management strategy viewpoints will converge, given comparable objectives. It is in this belief, that ecologists and ecosystem managers must work together to continually evolve more refined management plans as our basic knowledge of ecosystem function expands, that this conference was conceived.

All of the cosponsors of this symposium have programs that promote the use of basic science for a more rational management of the biosphere.

(1) SCOPE (Scientific Committee for the Problems of the Environment) is an international, nongovernmental organization established in 1969 to advance knowledge of environmental problems of global concern. It is the SCOPE Program 2 under which this symposium was sponsored. SCOPE 2 deals with dynamic changes and evolution of ecosystems with a program phase specifically devoted to fire ecology. This symposium is a United States contribution to this international program, as was the international conference on "Environmental Consequences of Fire and Fuel Management in Mediterranean-climate Ecosystems," held at Stanford University in August 1977.

(2) MAB (Man and the Biosphere) is a UNESCO program directed toward solving environmental problems of the biosphere. MAB Project 2, under which the conference was sponsored, is concerned with the ecological effects of different land uses and management practices on temperate and Mediterranean-climate landscapes.

(3) The Forest Service, U.S. Department of Agriculture, has among its charges the performance of basic and applied research in forest management, recreation, influences, watershed protection, and forest products utilization.

(4) The East-West Environment and Policy Institute is a part of the East-West Center in Honolulu, Hawaii, which has as one of its programs the assessment of natural resources and the environment for planning and assistance in developing countries.

The Hawaii conference was planned by F. H. Bormann of Yale University, Russell Burns of the United States Man and the Biosphere Program, Paul Risser of the University of Oklahoma, William Robertson IV of the National Resource Council's International Environmental Program Committee (IEPC) the U.S. coordinator of SCOPE, Scientific Committee for Problems of the Environment, and myself, at a meeting at Yale University in September 1977. A final planning meeting was held in Washington, D.C. in February 1978 with Bormann, Robertson, and me, joined by Richard Carpenter of the East-West Center, Miron Heinselman of the University of Minnesota, James Lotan of the Forest Service, and Suellen Pirages of IEPC. The conference organizers and participants acknowledge the considerable effort on the part of the staff of the East-West Center in providing the facilities and environment that made the symposium such a pleasant and successful undertaking.

Harold A. Mooney
Stanford University

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INTRODUCTION

For decades, the genius of Clemetsian ideas of succession and climax has dominated much ecological thinking and buttressed land-use policies that assigned catastrophic disturbance a relatively minor or infrequent role in naturally-occurring ecosystems. Quite properly, these ideas have received increasing criticism and much new evidence has been found to support the concept of recurring disturbance, particularly fire, as an an integral component of the structure and function of an increasing variety of ecosystems.

This change in ecological theory can only be regarded as a welcome advance in the science of ecology, but there is a worry that in our enthusiasm to unearth new facts we may be blinded to old truths and the pendulum of ecological thought may swing from one extreme to another. There is little doubt that, among the many recent and notable papers examining the role of fire in ecosystems, there are a surprising number that seem to pass the boundary of thoughtful scientific objectivity and assume the role of advocacy, in a legalistic sense, of fire as a factor in ecological systems. After nearly a half century of land-use policy that ruled out fire as a management tool and discouraged basic research in fire, a sense of advocacy on the part of many researchers is understandable. However, we must be clear in our thinking and be cognizant of the fact that advocacy is not part of the scientific method. In the long run, advocacy will only make more difficult the already difficult task of striking out the Clementsian isolation of fire as an ecological factor.

The planned purpose of this meeting was to place the role of fire in natural ecosystems in a balanced context by viewing a continuum of ecosystems from those where fire is a predictable and frequent event to those where fire is a rare occurrence. Although the synthesis of existing information on the role of fire in a range of ecosystems was a major objective of our conference, the primary goal was, through the verbal interaction of the participants at this meeting, to bring a new level of understanding to the role of fire in the function and management of ecosystems.

The tactical approach of the planning committee was to examine the role of fire frequency and intensity in the development of ecosystems and to explore the potential of fire as a tool in the management of ecosystems. Following this plan, the first session of the symposium was devoted to an examination of the effects of fire in regulating the distribution of ecosystems in space and time. Not only was the goal to examine environmental differences that give rise to regions characterized by an abundance of fire-dependent ecosystems and to other regions, such as the northern hardwood forest area of the White Mountains of New England, where relatively few ecosystems are fire dependent, but also to examine those factors that give rise to a local matrix of ecosystems in which fire plays a varying role in the maintenance of local ecosystem diversity. Understanding regional and local patterns is, of course, basic to the development of successful management schemes.

The second session was devoted largely to the reproductive and growth strategies of plants as they are evolutionarily modified by fire and as they contribute to the maintenance of fire-dependent systems. This discussion touches on the fact that some attributes of plants that make them successful in fire systems are not necessarily unique to fire systems and, in fact, might be adaptations to more general situations. One particularly interesting aspect of this session is the possibility that better understanding of the factors underlying the maintenance of plant populations in fire systems might open the possibility of breeding economically important plants to fire managed situations. At any rate, better knowledge of species strategies in fire-prone ecosystems is basic to success in using fire as a management tool.

Our third session was concerned with the role of fire in the structure and function of ecosystems. This is perhaps the most difficult of all areas of research both because of the complexity of ecosystems and because of the necessity of expensive, long-term study to provide a reliable guide to ecosystems behavior under fire regimes. Not only must we understand the behavior of the ecosystem itself, but also the effects of fire-generated outputs on interconnected aquatic and atmospheric systems.

Many difficult questions are involved at the ecosystem level, yet answers or reasonable approximations of answers to these questions are required if we are to design long-term fire-based schemes of landscape management. Not the least are questions concerning the maintenance of long term productivity in fire-based systems, which, in turn, require understanding of the rate of nutrient sequestration following nutrient losses due to volatilization or accelerated leaching. When the next fire cycle occurs, nutrient replacement must equal losses due to fire or the system will run down hill. That the system is not running down hill is an important point that researchers, who conclude that fire should be used as a tool in particular systems, must conclusively demonstrate to managers. Understanding of the nitrogen cycle, particularly nitrogen-fixation, would seem to be of prime importance in making this decision. Knowledge of the role of weathering rates within the ecosystem is probably of equal importance.

Another aspect of the fire question is attempting to better comprehend what the suppression of fire in fire-prone systems means in terms of ecosystem development. Will more or less productive systems result? Will changes in productivity be meaningful in terms of harvesting the products of the ecosystem or in terms of ecosystem regulation over biogeochemical cycles?

Other basic ecosystem questions concern the relationship between the rate of litter fall and the rate of decomposition. In some systems, apparently, decomposition does not equal litter production and as a consequence burnable organic matter often accumulates. On the other hand, in some humid forested systems, the rate of decomposition seems to come into equilibrium with the rate of litter fall and relatively little dead fuel accumulates within the ecosystem.

The role of geologic substrate in governing the development of fire-prone ecosystems is also of interest. For example, some fire-dependent ecosystems in the northeast are underlaid by deep deposits of quartz sand. Not only are these ecosystems subject to frequent surface droughts and, hence, frequent occurrence of conditions that promote fires, but the nutrient-poor substrate may give rise to vegetation with a low nutrient-to-carbon ratio for most elements. Nutrient-poor wood may be slow to decay and fuel may accumulate. Nutrient-poor leaves may contribute to podzolization and the development of a burnable A_0 horizon rather than a non-burnable A_1 horizon. In northern hardwood ecosystems, it is interesting to note that oligotrophic rocks can give rise to soil characterized by a heavy deposit of dead organic matter on the surface of the soil, while calcium-rich rocks in the same environment can give rise to soils where the overwhelming bulk of the soil organic matter is incorporated in the mineral soil. Thus, not only can geologic substrate influence the frequency of drought, but may also influence fuel accumulation and possibly the flammability of the vegetation itself.

In the long run, it is our understanding of ecosystem function, in addition to that of species behavior, that will allow us to establish durable and economically sound management plans that utilize fire as a tool.

Our final session focused on the use of fire in the management of landscape. Questions here are as complex as any and involve not only ecologic considerations but economic and social considerations as well. Managers are faced with the formidable task of translating basic research on the ecology of fire into landscape management

plans that are economically feasible and socially acceptable. All of these plans must be accomplished in a kaleidoscopically changing world situation in which the cost of energy, a basic ingredient of any landscape management scheme, and the concern over air and water pollution are both rapidly rising. The hope of the conference organizers was that our conference would enhance, at the very minimum, the two-way flow of information between managers and basic scientists.

F. H. Bormann
Yale School of Forestry and
Environmental Studies



SECTION I

ECOSYSTEM DISTRIBUTION AND STRUCTURE THROUGH SPACE AND TIME

The purpose of this section is to examine the relationship between fire frequency and intensity, and the distribution and structure of vegetation in five ecological regions. The goal is not simply to review the literature on the role of fire in different vegetation types, rather, the emphasis is on synthesis and an enhanced understanding of fire frequency and intensity as both a cause and effect of ecosystem characteristics.

Not all of the world's vegetation is considered in this analysis. The decision on how best to limit the scope of this section was based to some extent on the availability of sufficient literature to make meaningful comparisons between ecological regions, but it also represents an intended emphasis on North America. Consequently, the ecological regions selected were northern ecosystems, western forests and scrublands, grasslands, southeastern ecosystems, and tropical ecosystems.

Within each paper four general questions are addressed. How have fire regimes changed historically and what future changes are expected? How do different fire regimes affect the distribution of vegetation types? How have different fire regimes affected the development of such features of vegetation structure within those types as species composition, horizontal arrangement of individuals, or pattern, and the vertical arrangement, or stratification, of life-forms, growth-forms, and species? How do variations in vegetation structure affect fire regimes? These are difficult questions and, in some cases, the literature is too sparse or inconclusive to provide the authors in this section with adequate grounds for satisfactory answers.

T.M. Bonnicksen and N. L. Christensen



FIRE INTENSITY AND FREQUENCY AS FACTORS IN THE DISTRIBUTION
AND STRUCTURE OF NORTHERN ECOSYSTEMS

Miron L. Heinselman

Adjunct Professor of Ecology
University of Minnesota
Minneapolis, Minnesota

ABSTRACT

Most presettlement Canadian and Alaskan boreal forests and Rocky Mountain subalpine forests had lightning fire regimes of large-scale crown fires and high-intensity surface fires, causing total stand replacement on fire rotations (or cycles) of 50 to 200 years. Cycles and fire size varied with latitude, elevation, and topographic-climate factors. Some areas had smaller, less-intense surface fires at shorter intervals. The Great Lakes-Acadian forests had regimes of short cycle crown fires in near-boreal jack pine and spruce forests, combinations of moderate intensity short-interval surface fires and small-scale crown fires at longer intervals in red-white pine forests, and low intensity long-interval fires in hardwoods. Fire maintained the structure and pattern of the forest mosaic. These regimes still prevail in the far north. Elsewhere regimes and the forest mosaic are greatly modified by logging, man-caused fires, and fire suppression.

KEYWORDS: fire, frequency, regimes, northern, ecosystems

INTRODUCTION

The presettlement forests of much of northern North America were strongly fire-dependent, and in the far north many lightning-caused fires still play out their ecological roles, little affected by man. In many northern conifer forests the natural fire regime is one of large scale and intense running crown fires or severe surface fires--recurring only at intervals of 50 to 200 years or more. In some ecosystems the natural regime is one of periodic light surface fires at shorter intervals, with severe fires occurring rarely. But in either situation fire was the major agent that initiated and terminated vegetational successions; controlled the age structure, species composition and physiognomy of the vegetation; produced the vegetation mosaic on the landscape; and influenced nutrient cycles, energy flows, productivity, diversity, and stability throughout the ecosystem. Thus, if we are to understand the dynamics of most natural or man-modified forest ecosystems in the north, we must first understand fire's many roles. And it is equally important to identify those ecosystems that

experienced little fire, because in such cases we must look elsewhere for keys to natural system processes.

The purpose of this paper, then, is to identify the major ecosystems of northern North America, and then to:

- (1) Describe historical changes in fire regimes and their causes for each ecosystem.
- (2) Examine the role of fire in regulating vegetation structure and the variations in structural responses among ecosystems.
- (3) Examine the reciprocal influence of community structure on fire frequency and intensity.
- (4) Examine variations in ecosystem development (succession) under presettlement, contemporary, and managed fire regimes.

Each topic is discussed with the goal of relating what we know about presettlement conditions to any recent changes in fire regimes and to possible future fire management strategies. The hope is that in this way our theoretical knowledge of fire regimes and vegetation dynamics can be related to practical future problems.

PHYSIOGRAPHIC FACTORS

The vast regions occupied by northern ecosystems are far from homogeneous in geologic history, soils, topography, or climate. These variables must therefore be related to a continuum of changing ecosystems and fire regimes across the continent to understand important differences in vegetation and fire effects.

Extent of the Region

The region I am concerned with includes all of northern North America and the arctic islands beyond the continent, southward to a line roughly defined by southern Massachusetts, northern New Jersey and Pennsylvania, lower Ontario, northern lower Michigan (north of the Thumb), northern Wisconsin, northeastern Minnesota, the prairie margin in Manitoba, Saskatchewan, and Alberta, the high mountains of the Rockies south to Colorado, the interior mountain ranges of British Columbia and the Yukon, and coastal Alaska (where the hemlock-spruce forests are excluded). In the Rocky Mountains it includes only the higher elevations supporting subalpine forests and alpine tundra.

Geologic and Topographic Variables

A review of geologic and topographic variations is needed because topography exerts strong control over fire movements, and the prevailing topography of an ecosystem may account substantially for the scale and pattern of fire-controlled vegetation mosaics. Soils and bedrocks are also important because the moisture holding capacity of soils and the local drainage situation relate to drought responses in vegetation, and thus to differences in fire histories.

The geology, soils, and topography of most of the region can be quickly grasped by studying the maps and text in the appendix to Rowe's (1972) excellent Forest Regions of Canada. Unfortunately no comparable treatise yet exists for the United States. The largest single physiographic province involved is the Laurentian Upland or Canadian Shield--a vast region including much of Canada and most of the Minnesota, Wisconsin, and Michigan areas treated here. It is an enormous plain of generally low relief (500 to 2,500 ft, 150 to 760 m), with sharply broken knob and ridge topography developed on Precambrian bedrocks--largely granite, quartzite, and other siliceous rocks, covered by thin stony and sandy glacial tills or outwash, and local areas of lacustrine clays.

There is an extensive network of large and small lakes, ponds, streams, and bogs. The Hudson Bay lowlands province is a flat region of glacial and marine sediments covered by a complex of raised bogs and patterned fens, broken intermittently by major rivers.

In western Canada there are two regions of concern: the Interior Plains and the Rocky Mountains division of the Cordilleran province. The former is a broad lowland running northward from the Saskatchewan and Alberta prairies, culminating in the Mackenzie Valley. It is a region of rolling plains and low hills, broken occasionally by low mountains. Bedrocks are mostly limestones, shales, and sandstones. There are extensive areas of lacustrine clays and vast muskegs in the north. The Canadian Rockies are steep and reach elevations of 12,000 ft (3 700 m), but most of the vegetation occurs below 7,000 ft (2 100 m) and timberlines decline northward from near 7,000 ft (2 100 m) in southern Alberta to 3,000 to 4,000 ft (1 000 to 1 200 m) in the Yukon. Bedrocks are mostly sedimentary.

In the United States the Rockies reach elevations of 14,000 ft (4 300 m) in Colorado and the timberlines climb gradually to the south, reaching 11,500 ft (3 500 m) in that State. The geology and topography of Alaska are complex, but the ecosystems treated here mostly occur below 5,000 ft (1 500 m). The Alaska Range contains the highest mountains in North America, but most of the land above 5,000 ft (1 500 m) is rocky barren or permanent ice and snowfields. Timberlines decrease to 2,500 ft (800 m) or less in the Brooks Range, and tundra reaches sea level at the Bering Sea and Arctic Ocean. (A summary of relevant physiographic factors in Alaska is available in Joint Federal-State Land Use Planning Commission for Alaska [LUPCA 1973].)

Permafrost is an important environmental factor in much of northern Canada and Alaska and it interacts strongly with fire effects on certain sites. Generalized permafrost maps for Canada and Alaska can be found in Rowe (1972) and LUPCA (1973).

In the northeastern United States the southern limit of the ecosystems I will discuss is reached in the highlands of Massachusetts, the White Mountains of New Hampshire, the Green Mountains of Vermont, the Catskills and Adirondacks of New York, and on the Allegheny Plateau in Pennsylvania. Only the Adirondacks, the White Mountains and Mt. Katahdin in Maine exceed 5,000 ft (1 500 m) in elevation, but in those areas timberline occurs near 5,000 ft (1 500 m). New Brunswick, Nova Scotia, and the Newfoundland islands really belong to the Appalachian province. Their landscapes are generally undulating to rugged and controlled by sedimentary bedrocks, but granitic intrusions also create certain highlands. Many of the highest New England mountains are formed by massive granitic intrusions.

Climatic Variations in Time and Space

Many of the otherwise perplexing differences in fire effects between ecosystems can be explained through comparison of climatic variables. I can do little here but cite references, and paint a broad continental picture. For Canada, Rowe's (1972) maps and data summaries provide an invaluable quick overview of climate; for details see Thomas (1953). For Alaska see Viereck and Little (1975). For the Rocky Mountain, north central, and northeastern States consult Visher (1954), Fowells (1965), Lull (1968), and Merz (1978). For a continent-wide overview of fire-weather factors see Schroeder and Buck (1970).

From the fire-weather standpoint the entire northern region discussed here has two important climatic features: (1) winters are long and cold, and ground is normally snow-covered for 4 to 8 months, and (2) summers are a season with substantial rainfall in most years; in fact, in most of the region the "normal" climate is winter dry-summer wet--with more than half of the annual precipitation coming as rain in the warm season. These features mean that fires cannot burn during the cold season because of snow cover, and that "normal" summers are usually too wet for major fires.

They also mean that grasses, sedges, and leafy deciduous trees, shrubs, and herbs are normally in green, high-moisture stages during summer, and that a brief low-moisture vegetation "cured" stage occurs only in spring and fall, shortly before and after the season of snow cover. Fires are therefore most likely to spread rapidly in spring and fall in "normal" years. These facts contrast sharply with the summer-dry climates of Washington, Oregon, and California.

However, actual fire records for many areas show that major fires do occur in midsummer. The reason is that in conifer forests, particularly where there is little herbaceous undervegetation and little development of broadleaf shrub or tree strata, major fires are possible during extended summer droughts. Droughts sufficiently severe to permit major summer fires may occur in any one locality only at very long intervals, perhaps 20 to 100 years or more, but this feature of most northern climates may be responsible for the vegetation and fire regimes of vast areas. I will return to that thought later.

Another feature of northern climates is a generally lower incidence of thunderstorms compared to more southerly regions. There is a more or less regular decrease in thunderstorm occurrence from south to north over the North American continent, although mountain ranges introduce complexity to that pattern. Nevertheless, some thunderstorms do occur up to the northern limit of trees, and even northward into tundra regions. But because rains accompany most thunderstorms, and most such storms occur in midsummer when soil moisture is often still adequate and vegetation is lush and green, the probability of lightning igniting significant fires is usually low. In fact, Schroeder and Buck (1970) show an incidence of fewer than 15 reported lightning fires per million hectares per year for most of the north. How, then, can lightning be an important fire source? The answer is that forest fires need not be frequent to be ecologically significant. They only need be severe enough and certain enough that sooner or later a fire will consume a given vegetation before its fire-dependent species are lost through succession.

One more generalization is relevant. It is that east of the Rockies and the Alaska Range there is a general and systematic two-way precipitation gradient: average annual total precipitation increases eastward and decreases northward. This is true for warm season rainfall as well as winter snowfall. At the same time, precipitation effectiveness increases northward due to decreasing temperatures. The net effect produces a distinctly drier climate in the western Canadian and Alaskan boreal forests compared to that of regions east of Hudson Bay, and in Minnesota compared to New England. For example, total annual precipitation at Dawson in the Yukon averages only 13 inches (330 mm) while at Island Falls, Saskatchewan, it averages 19 inches (483 mm), at Pickle Lake, Ontario, 27 inches (686 mm), and at Mistassini Post, Quebec, 32 inches (813 mm)--all in climates not drastically different in annual temperatures (Rowe 1972). And at International Falls, Minnesota, the total annual precipitation averages 24 inches (610 mm), while in northern New England it averages 42 inches (1 067 mm). Furthermore, most western and northwestern regions experience substantially more clear and sunny summer days, and northward also longer days than do eastern regions. The cumulative effect of these differences produces summer climates much more conducive to the spread of fires in the northwest than in the east.

Much of the north is geologically young--having been covered by Pleistocene glaciation until 6,000 to 20,000 years ago (Bryson and others 1969; Wright 1971; Wright 1976). Paleoecological evidence indicates that post-glacial vegetation movements in response to climatic change have been major and often rapid (Larsen 1965; McAndrews 1966; Wright 1970, 1972; Webb and Bryson 1972; Jacobson 1976; Swain 1973, 1978). Interactions between climatic change and fire occurrence may account for some post-glacial shifts of vegetation boundaries--such as the retreat of the treeline in parts of the Canadian subarctic (Larsen 1965, Ritchie and Hare 1971).

MAJOR ECOSYSTEMS OF NORTHERN NORTH AMERICA

The balance of this paper considers the relationship between fire regimes and the distribution and structure of the following broad ecosystems:

Arctic and Alpine Tundra

According to Rowe (1972) tundra can be defined as the low, treeless vegetation of high latitudes and high altitudes, usually characterized by lichens, sedges, and dwarf shrubs. Such vegetation occupies vast areas beyond the northern limit of trees from Labrador northwestward to Alaska. The alpine tundras of the Canadian and American Rockies and of a few of the highest eastern mountains will also be considered here. Küchler (1966) lists one tundra type (Agrostis, Carex, Festuca, Poa--type 45) for the western mountains, but seven types for Alaska, including his essentially treeless Alder Thicket and Muskeg types.

Subalpine Forests

A broad belt of subalpine northern forest in the Rocky Mountain system begins in northern British Columbia at elevations of 2,500 to 5,000 ft (800 to 1 600 m), and climbs gradually southward to a zone between about 8,000 to 11,500 ft (2 400 to 3 500 m) in central Colorado. Its most characteristic trees are Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and lodgepole pine (Pinus contorta, var. latifolia). Quaking aspen (Populus tremuloides) is also abundant in certain areas, and in British Columbia and Alberta, white spruce (Picea glauca) and white spruce-Engelmann spruce hybrids replace Engelmann spruce in many northern and eastern areas. The black spruce (Picea mariana) also occurs from Jasper Park northward. Near treeline the whitebark pine (Pinus albicaulis) is common; southward its place is taken by limber pine (Pinus flexilis). Included in my discussion will be the forests of Rowe's (1972) S.A.1 Section (East Slope Rockies) and the eastern portions of his S.A.2 Section (Interior Subalpine) in Canada, plus Küchler's (1966) type 14 (Western Spruce-Fir Forest) in the American Rocky Mountains. In Alberta and northern British Columbia these ecosystems merge imperceptibly along their eastern margins with the Boreal Forest regions of Rowe (1972), and at their lower altitudinal limits in the Rockies they merge with Küchler's (1966) type 17 (Pine-Douglas-fir Forest), and type 11 (Douglas-fir Forest). Küchler's type 17 and 11 are not included in the ecosystems discussed here.

There are also limited areas of very different subalpine forest near the summits of the highest mountains in the northeastern United States--the Adirondacks, the White Mountains, and Mt. Katahdin. The principal tree is balsam fir (Abies balsamea), which often forms nearly pure stands just below timberline at elevations between about 4,000 and 5,200 ft (1 200 and 1 600 m). Red spruce (Picea rubens) also occurs.

Boreal Forests

I restrict the term Boreal Forest here to the vast region defined by Rowe (1972), plus its extensions into Alaska. It crosses Canada from Newfoundland and the coast of Labrador to Alaska, occupying all of the forested interior, and finally reaching the Bering Sea and Arctic Ocean. In Canada, the Boreal Forest comprises most of the forested area east of the Rockies, forming a continuous belt several hundred miles wide northward from Rowe's Acadian and Great Lakes-St. Lawrence Forest regions and his Aspen-Oak and Aspen Grove divisions of the boreal region (here considered separately as the Aspen Parkland) to the tundra. The white and the black spruces are characteristic species; other conifers are tamarack (Larix laricina), balsam fir, and jack pine (Pinus banksiana)--prominent in the eastern and west-central portions, and subalpine fir and lodgepole pine in the extreme western and northwestern parts. Although the

forests are primarily coniferous, there is a general admixture of broadleaved trees such as paper birch (Betula papyrifera) and its varieties, quaking aspen (Populus tremuloides) and balsam poplar (Populus balsamifera)--the latter two playing an important part in the south-central portions. The proportion of black spruce and tamarack rises northward, and with increasingly severe climatic and soil conditions the closed forest gives way to subarctic open lichen-woodlands which finally merge into tundra. In the southeast there is a considerable intermixture of species from the Great Lakes-St. Lawrence Forest such as eastern white and red pines (Pinus strobus and P. resinosa), yellow birch (Betula alleghaniensis), sugar maple (Acer saccharum), black ash (Fraxinus nigra), and northern white cedar (Thuja occidentalis).

Aspen Parkland

In northwestern Minnesota and west-central Canada, the southern edge of the Boreal Forest meets the cultivated and natural prairies in a long arc-like front extending westward to the foothills of the Rockies in Alberta. Here the broadleaf trees of the southern boreal forest produce a region characterized by savanna-like patches of forest in a prairie matrix. The region includes Rowe's B.16 (Aspen-Oak Section) and B.17 (Aspen Grove Section) and some of Kuchler's type 72 (Oak Savana). From Minnesota to Saskatchewan quaking aspen mingles with balsam poplar, bur oak (Quercus macrocarpa), and along the river valleys also with green ash (Fraxinus pennsylvanica), American elm (Ulmus americana), boxelder (Acer negundo), and in the east basswood (Tilia americana) and black ash (Fraxinus nigra). Westward, quaking aspen becomes the principal tree, with balsam poplar and paper birch occasional. Northward, this transitional region merges gradually with closed deciduous forests of aspen and birch, and finally with the coniferous forests of the full Boreal Region.

Great Lakes-St. Lawrence and Acadian Forests

From southeastern Manitoba and Minnesota eastward to Maine, New Brunswick, and Nova Scotia there is a forest belt containing elements of both the boreal forest and the main deciduous forest region of the eastern United States. It also contains characteristic species of its own--notably eastern white pine, red pine, and in the east, eastern hemlock (Tsuga canadensis), red spruce, and others. I am including here all of Rowe's (1972) Great Lakes-St. Lawrence and Acadian forest regions, and Kuchler's (1966) types 84 (Great Lakes Spruce-Fir Forest), 85 (Conifer Bog), 86 (Great Lakes Pine Forest), 87 (Northeastern Spruce-Fir Forest), 98 (Northern Hardwoods-Fir Forest), 99 (Northern Hardwoods-Spruce Forest), and for comparative purposes also 97 (Northern Hardwoods).

These forests form the southern limits of the ecosystems that I will discuss. Along the southern edges of this transition from boreal forests to the eastern deciduous forests, the principal trees are sugar maple, yellow birch, red maple (Acer rubrum), beech (Fagus gradifolia), white oak (Quercus alba), white ash (Fraxinus americana) and formerly American elm. White pine and hemlock also mingle widely with these hardwoods in the south. Of course, the whole vegetation of northeastern North America is really a continuum from the largely coniferous boreal forests of the far north to the broadleaf deciduous forests of the so-called northern hardwoods region.

HISTORICAL CHANGES IN FIRE REGIMES AND THEIR CAUSES

The kind of fire history that characterized an ecosystem can be summarized as its fire regime. The elements of a fire regime are (1) fire type and intensity (crown fires or severe surface fires vs. light surface fires), (2) size (area) of typical ecologically significant fires, and (3) frequency or return intervals typical for specific land units. Seven kinds of fire regimes can be distinguished for forest ecosystems:

- 0 = No natural fire (or very little).
- 1 = Infrequent light surface fires (more than 25-year return intervals).
- 2 = Frequent light surface fires (1- to 25-year return intervals).
- 3 = Infrequent, severe surface fires (more than 25-year return intervals).
- 4 = Short return interval crown fires and severe surface fires in combination (25- to 100-year return intervals).
- 5 = Long return interval crown fires and severe surface fires in combination (100- to 300-year return intervals).
- 6 = Very long return interval crown fires and severe surface fires in combination (over 300-year return intervals).

In presettlement times combinations of these regimes were typical of many ecosystems. For example, in red pine in the Lake States the regime was a combination of 2 or 3 and 5 in most localities. Regimes also varied with vegetation types and physiographic sites within biogeographic regions. For example: the jack pine type in the Boundary Waters Canoe Area was subject to regime 4 or 5 on most sites (as opposed to the 2 or 3 + 5 regime for red pine) (Heinselman 1973). The purpose here is not to set up a precise classification but to make it possible to discuss important differences in the way fire influences ecosystems.

The average time required for a natural fire regime to burn over an area equivalent to the total area of an ecosystem is somewhat analogous to the forester's "rotation." It can be called the Natural Fire Rotation (Heinselman 1973). In the natural world fire was really not that orderly, however, because each vegetation type and physiographic site tends to have its own characteristic return interval, and in many ecosystems fire is a semirandom process. This means that some areas will be skipped by fire for very long periods, while others may burn two or more times during a rotation. But the fire rotation concept is still useful for comparing the role of fire in different ecosystems. Van Wagner (1978) uses the term fire cycle for the same concept. With this background let us consider the known history of fire in each major northern ecosystem.

Arctic and Alpine Tundra

Most of the arctic and subarctic tundra regions of Canada and Alaska are still essentially pristine environments, with very sparse human populations, and little man-related activity that might alter natural fire regimes. This picture may now be changing rapidly from the Mackenzie delta westward across the northern Alaskan coast because of road construction and onshore and offshore oil exploration and drilling. There are also a few remote enclaves of mining activity.

There has been little research on the role of fire in arctic tundra, partly because fires are not common. However, both man-caused and lightning-ignited fires do occur, and the recent work of Wein (1976) provides some basis for generalizations. Tundra fires are unknown, and probably cannot occur in the Canadian Arctic Islands Archipelago because biomass there is simply too sparse and discontinuous. But in Alaska, in the Canadian Districts of Mackenzie and Keewatin, and in northern Quebec Wein has verified numerous tundra fires, many lightning caused. Lightning fires may occur in groups following a dry electrical storm if there is suitable fuel over a considerable area.

More fires occur near the forest--tundra ecotone, and they often spread farther if a few scattered spruce trees are available to aid in spotting across fuel discontinuities. But in many treeless tundra areas the fuel is so sparse and discontinuous that ultimate fire size is very small. Wein (1976) reports many fires in the 1 to 100 hectare size range, however, and several in the thousands of hectares. The largest reported fires were a group of 3 on the Seward Peninsula in Alaska that together burned 16,000 square kilometers of cottongrass tussocks. July and August are the most common months for lightning fires. Man-caused fires do occur and, with increasing human occupancy, could become significant.

Fires in open subarctic spruce stands at treeline might sometimes convert such forests to tundra for very long periods (Black and Bliss 1978). Larsen (1965) reports that this occurred north of Ennadai Lake in the District of Keewatin--where two buried charcoal strata in tundra have been carbon-dated at 880 and 4,000 years B.P. Later work by Ritchie and Hare (1971) indicates that a general retreat of treeline has occurred in northern Canada in the past 5,000 years. Climatic deterioration is the primary cause, but interactions with fire were involved.

Fires in alpine tundra occur near treeline in the Northern Rocky Mountains, and at least some of the burns may convert timberline forests into semipermanent tundra communities because trees reestablish very slowly in such environments (Stahelin 1943, Billings 1969). Habeck (1970) quotes Ayres as describing several treeline burns in Glacier National Park about 1900. However, Tande (1977) found that fires were much less frequent in the higher elevation spruce-fir forests near treeline in Jasper National Park, Alberta, than in the main lodgepole pine forest belts below. Several areas near treeline, especially on north- and east-facing slopes, yielded no clear evidence of past fires. His data suggest that on the average, fires running from treeline on into tundra would occur only at intervals of hundreds of years, and on some sites only rarely, if at all. How extensive such fires were within the tundra communities themselves is not clear.

This scanty evidence provides no firm basis for generalizing on the presettlement fire regimes of Rocky Mountain tundra ecosystems. About all that can be said is that fires were a factor in creating or maintaining some tundra areas, but that fire was probably not a dominant influence in most tundra ecosystems. In the last 50 years fire control has become more effective in the Rockies, and significant fires in tundra are now even less likely than in the past. Many hikers now travel the high country in the National Parks and Wilderness Areas of the West, and some use campfires, but I am not aware of data on such activities as sources of tundra fires. The probable cumulative effect of man's recent activities on alpine tundra fire regimes is that fire exclusion may now be causing a net reinvasion by trees of old fire-created "tundra" areas.

Subalpine Forests

The "subalpine" forests of the Rockies included here comprise a wider elevational band of vegetation than is often covered by the term subalpine. I include the lodgepole pine zones and aspen zones, down to the ecotone with Douglas-fir, as well as the usual upper spruce-fir zone. It is the ecological equivalent of the boreal forest of Canada, translated to the Rocky Mountains. I do this because this entire elevational zone clearly fits the "northern ecosystem" concept, and it would only complicate the discussion to break these forests into boreal and subalpine classes.

Five studies of the fire regimes of Rocky Mountain subalpine ecosystems based on dendrochronologies obtained from sections of fire-scarred trees are available. They include the pioneering study of Clements (1910) near Estes Park, Colo., Houston's (1973) study in the Mammoth Hot Springs area of Yellowstone National Park, Wyo., Gabriel's (1976) study in Montana's Bob Marshall Wilderness' Danaher drainage, Arno's (1976) study of three areas near the east slopes of Montana's Bitterroot Range, and Tande's (1977) study of an 18-mile (29-km) segment of the Athabasca Valley in Jasper National Park, Alberta, centered around Jasper townsite.

Tande's (1977) study produced a detailed stand origin map of his entire 43 200 ha study area, in addition to a chronology of fires from 1665 to 1975 based on 664 fire scar dates and thousands of stand age determinations. I spent a week in Tande's area in company with him in 1975. My field work on that trip supports and supplements (in a very small way) his findings. His study covered the full subalpine zone from valley floor to treeline and included some Douglas-fir savanna below the subalpine. In the Jasper area settlement did not begin until 1892, and fire suppression became

effective about 1907 when the Park was established, so the period of strong human influence without fire control was brief.

"Major fires" (covering more than 50 ha, or 1.2 percent of the study area) occurred in 1908, 1906, 1905, 1904, 1889, 1888, 1884, 1883, 1880, 1869, 1863, 1861, 1858, 1847, 1846, 1837, 1834, 1807, 1797, 1780, 1758, 1737, 1727, and 1714. Most of the forests of today originated after the fires of 1889, 1847, and 1758. The mean fire return interval (MFRI) for the whole study area between 1665 and 1907 (the presuppression period) was 5.5 years. The MFRI for "major fires" was 8.4 years; for fires covering more than 50 percent of the study area it was 65.5 years; for 50 ha blocks of lodgepole pine forest it was 26.8 years; and for the upper subalpine Englemann spruce-subalpine fir-lodgepole pine zone it was 74 years. The fires of 1758, 1847, and 1889 occurred during severe droughts according to a dendroclimatology analysis. Some of the study area is occupied by grassland and Douglas-fir savanna at the lower elevations, so the most relevant MFRI figures are those for lodgepole pine stands and the upper subalpine zone.

Many lodgepole pine stands in this area contain trees of two or more age classes, each dating from separate fires--a condition particularly common at the lower elevations adjacent to grassland or Douglas-fir savanna. But at the higher elevations, dense and nearly even-aged stands of lodgepole pine were more common--often dating closely from the last fire. The fires of 1888 and 1889 covered 81 percent of the study area, and more stands now date from those fires than from all others combined. Most of the 1889 fires were of medium to high intensity.

There is clear evidence that the higher elevation forests were subject to fewer, but higher intensity fires than were lower elevation forests. Creeping surface fires burned through some low elevation lodgepole pine stands without killing many trees, but there is little evidence of such fires on the higher and steeper slopes. In many places the subalpine forests were consumed to treeline, but on the other hand there are several large areas of Englemann spruce-subalpine fir and whitebark pine forest on north- and east-facing slopes lacking any apparent evidence of past fires.

Tande's data thus document a presettlement fire regime for the lodgepole pine-spruce-fir zone of short recurrence interval (65 to 100 years) severe surface fires and crown fires in most of the steeper slope and higher elevation forests--nearly, but not quite to treeline. Near treeline fires were less frequent, and some areas seldom, if ever, burned. Near the valley floor on flatter terrain many pine stands experienced low to medium intensity surface fires that killed only portions of such stands. Taking the Athabasca Valley near Jasper as a sample of the region, it appears that the ecologically most significant fires were quite large in area, burning thousands of hectares from valley bottom to near treeline--and perhaps, as in the fires of 1889, jumping from one subdrainage to another, eventually working up and down the valley for many kilometers. We cannot tell how much of the 1889 burn resulted from a single fire, but most likely there were many separate fires and multiple starts. There were many skipped areas in the 1889 and other large fire areas, so it is easy to see how seed sources for spruce and fir were preserved. Lodgepole pine in this region is mostly of the closed-cone variety so living trees were not needed for its reproduction.

Lightning is a widespread and adequate source of ignition to account for this presettlement fire history, but the actual causes of these fires are unknown. Lightning fires occur from June through September, but most fires of significance occur in July or August.

Tande's study area has not experienced large-scale fires since suppression began in 1907, and the present fire cycle, if continued, would be many thousands of years. North of Jasper Park, in the northern Alberta and British Columbia Rocky Mountain system fire control has been less effective until quite recently, but no formal studies

of the fire regime are available. Southeast of Jasper in Alberta's Rocky Mountain Forest Reserve, Day (1972) has analyzed forest inventory stand age data for extensive areas of lodgepole pine and spruce-fir forests on the east slopes of the Rockies. These data indicate an increase in length of average fire cycles for lodgepole pine-dominated subalpine forests from about 55 years before control began (about 1911) to about 450 years since then. These are generalized estimates, and the variability that must have existed within such a large region is obscured.

In the Montana Rockies Arno (1976) and Gabriel (1976) have documented fire regimes in lower subalpine lodgepole pine stands that were similar to those found by Tande at Jasper. Many stands had regimes of frequent light to moderate surface fires that did not kill the entire stand--leading to multiaged stand structures. Recurrence intervals were extremely variable, but many stands were visited by fires at intervals of 10 to 40 years. At middle and upper elevations Gabriel found more evidence of severe surface fires and crown fires that had killed out large stands and brought in whole new age classes. He suggested a fire rotation of about 150 to 200 years for his entire study area, but that does not include much reburning of lower elevation stands, which seemed to occur on a shorter cycle of 15- to 45-year intervals in any one stand. Arno found considerable reburning without stand kill even at higher elevations, but his study areas were on the edges of major mountain ranges, and may not be typical of many mountain slopes deeper within a given range. Both Gabriel and Arno obtained many of their fire scar dates from ponderosa pines in mixed lodgepole pine-Douglas-fir-ponderosa pine stands transitional to the montane forest zone, and thus not really part of the subalpine zone discussed here.

In both Gabriel's and Arno's study areas, 1889 was a major fire year, as it had been at Jasper in Tande's study. But in these Montana areas a much smaller proportion of stands dated from 1889 burns, and the whole stand age structure was more complex than at Jasper. Habeck (1970) quotes a report by H. B. Ayres noting large 1889 burns in what is now Glacier National Park, Montana. Undoubtedly 1889 was a year of severe regional drought that extended at least from Montana and Idaho northward to the Jasper Park region of Alberta. Such years may well have accounted for much of the ecologically significant burning in presettlement times in the subalpine zone.

Arno's fire chronology, based on 889 fire scars from 171 trees, documents some 137 fire years in the period 1948 to 1366, and Gabriel's chronology gives 79 fire years for the period 1946 to 1749, based on 222 individual scars. In Gabriel's area the fires of 1919, 1910, and 1889 were clearly the most widespread. Both chronologies leave no doubt that fire frequencies similar to those at the time of settlement extended far back into prehistory. Many of Gabriel's stands dated from fires in 1809 and 1803, and some of his oldest stands originated after fires in 1714, 1729, 1749, 1759, and 1784-89. (Some of these same stand origin dates are common in Minnesota red pine.)

Farther southeast, Houston (1973) in Yellowstone Park, Wyo., and Loope and Gruell (1973) in Grand Teton National Park, Wyoming, have documented the fire history of additional lodgepole pine forests. Again, Houston's fire scar chronology came from lodgepole pine-Douglas-fir savanna at the lower margin of the subalpine zone as here discussed. But both Houston's work and the observations and limited fire scar work of Loope and Gruell indicate that many presettlement fires in the lodgepole pine forests of the Yellowstone-Grand Teton region were of the creeping surface fire type that often scarred trees without killing out entire stands. Many stands are still open and parklike, and lodgepole pine regeneration is still common in such stand openings even without fire. Furthermore, there are many stand boundaries, suggesting that at least some fires were small in area. Many lodgepole pine stands in the region have non-serotinous (open) cones, suggesting genetic adaptation to nonlethal fires as suggested by Lotan (1967). My own general observations in higher elevation stands suggest that lethal crown fires did frequently occur in some drainages, however. The 1889 fire year was not recorded in Houston's study area, but the 1803 and 1758 fires were, as

was 1863--another common fire year in Minnesota red pine. Houston's chronology extends from 1893 to 1525--again documenting a very long presettlement fire history.

Clements (1910) found similar evidence in the Colorado Rockies in what may well be the first scientific use of fire scar chronologies to document fire history. In his study area on the Colorado Front Range, 1864 was the major fire year in the whole area, more stands dating from burns of that year than from all others. Apparently most lodgepole pines had serotinous (closed) cones in his study area, and most fires were lethal crown fires or severe surface fires that resulted in total stand renewal. Wellner (1970) has reviewed the history of fires in the Northern Rockies, and he concludes that large-scale, lethal stand-killing fires that regenerate whole watersheds are the rule rather than the exception. The review by Habeck and Mutch (1973) and the newer studies just reviewed here make it plain that both kinds of fire regimes were common, however (also see Brown 1975; Alexander and Sandberg 1976).

Gabriel, Arno, Houston, and Tande all found that fires nearly or totally ceased early in this century in their study areas. Only Gabriel's area (in a remote wilderness drainage) showed substantial burning since about 1915, and even he found no fires since 1944. Thus the fire protection efforts of the last 60 to 70 years have clearly removed a major natural environmental factor from these forests, and in the short term at least, fire exclusion has become a virtual reality.

Logging in the Rocky Mountain subalpine forests as defined here has not been very widespread until quite recently. And even now vast areas remain untouched, either because they are within National Parks and Wilderness Areas, because their forests are not yet economically exploitable even for pulpwood, or simply because the demand for timber has still not reached many inaccessible areas. Logging has been more widespread in Colorado, Wyoming, and Montana than in the Canadian Rockies, and where logging has occurred it is mostly clearcutting (Lotan 1975). Fire is often used in slash disposal, but many cutover areas have not been so treated (Roe and others 1971). Where broadcast-burning has been used in slash treatment, postfire regeneration depends heavily on subsequent seeding or planting by man, and on the proximity of natural seed sources. This is also true of untreated areas, of course, although more advance growth may survive in such areas. In general, the postlogging regeneration of lodgepole pine stands has been more successful than that of Engelmann spruce and subalpine fir.

Man's major impact on natural fire regimes, then, has been to lengthen fire recurrence intervals for most regions through fire control, and in some areas to substitute logging and slash burning for natural fire. In many areas there has clearly been a major reduction in the number and area of large-scale high-intensity burns, particularly in the last 40 years, and at lower elevations also periodic light surface fires. The effect of such changes in many areas perhaps has been mainly to postpone fires, because the even-aged postfire forests are still present on the landscape--waiting for ignition, and fuels and flammable understories are increasing. The average age of postfire stands has therefore lengthened beyond the presettlement pattern (i.e., fire rotations have lengthened dramatically for whole regions). But fires do still occur in many areas, and some are still large. I cannot make good quantitative estimates of these changes in fire rotations, but they are orders of magnitude longer than presettlement rotations.

The quaking aspen forests of the Rockies present special problems. In the north some stands occur at lower elevations on warm south- and southwest-facing slopes, near or just above Douglas-fir savanna, and often associated with open "parks" within lodgepole pine areas. But in Colorado there are extensive even-aged forests of aspen between about 7,500 and 10,000 ft (2 300 and 3 000 m), often on cool-moist benches and slopes. Virtually all natural stands seem to be of postfire origin, but the kinds of fire regimes that produced these stands are not well known. Most regeneration following fire is by root-suckering (Pearson 1914, Fowells 1965, Jones 1973). Many stands are nearly

pure aspen, although some have understories of spruce and fir and intermingled patches of lodgepole pine. Probably the presettlement fire regime was one of long return interval (50 to 150 years?) severe surface fires (crowning is rare in nearly pure aspen). A clear picture of the typical size of past fires is not available, but many such fires probably occurred in the same major drought years that produced large-scale fires in the nearby lodgepole pine and spruce-fir forests. Verification of this hypothesis through fire scar and stand origin dating is possible. Since the advent of fire protection there have been few extensive fires in aspen because such fires are easily controlled. Thus man has drastically lengthened the natural fire rotations for most Rocky Mountain aspen forests--so much so that replacement through succession or unnatural stand breakup without fire seems inevitable in many areas.

The subalpine forests of stunted balsam fir and red spruce near treeline on the high mountains of New York and New England have had a very different fire history. There, the climate is cool, wet, and humid much of the summer, total precipitation is high (45 to 55 inches [1 100 to 1 400 mm]), and the mixed hardwood-conifer forests of the lower slopes are not very fire prone. Electrical storms are common, but most are accompanied by significant rains, and forest fuels are almost always moist. Thus these forests have little or no fire history on most sites, and one must look elsewhere for an understanding of ecosystem dynamics (Sprugel 1976). Logging, slash burning, and/or land-clearing have occurred on the lower slopes of most of these mountains over the past 300 years, but even those activities did not produce widespread burning of most subalpine forests. The subalpine stands themselves are of little commercial value and most have not been exploited.

Boreal Forests

The boreal forests of Canada and Alaska are so vast that subdivision is essential and even then only gross generalizations covering hundreds of millions of hectares are possible. On the other hand, these forests are relatively simple in floristics and vegetation, so hopefully what follows will at least establish the range of fire regimes.

MAIN CANADIAN BOREAL FOREST DIVISION

This division includes all of Rowe's (1972) Boreal Forest except the Aspen Parkland Region, the Foothills Sections (B.19a,b,c), the Upper Liard (B.24), Stikine Plateau (B.25), Central Yukon (B.26b), Kluane (B.26d), Eastern Yukon (B.26c), and Dawson (B.26a) Sections. The last is discussed separately along with interior Alaska. The rest of the above exceptions (other than Aspen Parkland) are discussed as a group because of the influence of Cordilleran vegetation elements in their floras.

The main transcontinental boreal forest of Canada is an enormous region of remote forest land, several hundred million hectares in extent. Only about a quarter of its area has yet been subjected to logging or other direct forest exploitation. Many undeveloped northern areas are still without roads or railroads, and only scattered native villages or mining towns are possible sources of direct human impact. Very few people any longer live "in the bush," and much of the area is therefore totally uninhabited. In Quebec and eastern Ontario the band of boreal forest under exploitation for pulpwood is wider, in places approaching the margin of the subarctic open spruce-lichen woodlands (Rowe's Northern Transition Sections). Farther west, in northwestern Ontario, Manitoba, Saskatchewan, and Alberta, the band of potentially exploitable but still untouched boreal forest becomes much wider.

Fire protection has existed in many developed areas for several decades, and even in the more remote areas there has been an attempt to control fires near settlements for 20 to 30 years. But in most of the remote north, beyond current timber license areas, fire control is either not attempted, or has had little impact because of the

vastness and remoteness of the region. Those areas are still essentially pristine environments with respect to natural lightning-caused fire regimes, and the available fire records indicate that lightning-started fires are responsible for most of the annual burn area.

Throughout the boreal forest, wherever unexploited forests still exist in large blocks, the dominant fire regime is one of short to relatively long return interval crown fires or severe surface fires--the return intervals for specific forest stands averaging perhaps 50 to 150 years in various regions. And most ecologically significant fires are large in area--often thousands of hectares and some hundreds of thousands of hectares. There are some areas where intermittent creeping surface fires are also important, but these are exceptions. The best data on long-term fire frequency come from a group of studies centered in northern Saskatchewan and Alberta and northward along the Mackenzie River to the arctic coast, prompted by pipeline investigations and controversy over the role of fire on caribou winter ranges (Scotter 1964, 1967, 1972; Rowe and Scotter 1973; Rowe and others 1974; Rowe and others 1975; Johnson and Rowe 1975, 1977; Bergerud 1974; and Kelsall, Telfer, and Wright 1977).

Johnson and Rowe (1975) have documented the fire regime from 1966 to 1972 for a 26-million-acre (10-million-hectare) unit of boreal forest north and east of Fort Smith, N.W.T. (largely in Rowe's B.27--Northwestern Transition section). A total of about 1.6 million acres (650 000 hectares) burned in the 7-year period, roughly 0.9 percent of the total area annually. Lightning caused 85 percent of all fires and accounted for 99.9 percent of the area burned. Scotter (1967) analyzed the 1961-64 fire reports for a large group of protected areas (some near settlements) in the N.W.T., northeastern Alberta, and northern Saskatchewan and Manitoba, and found the annual burn rate to be about 0.7 percent, with 72 percent of all fires lightning-caused. These data suggest an average lightning-fire rotation of about 120 years. Johnson and Rowe believe that fire frequency is higher in the closed boreal forest in the southwestern portion of the study region, and considerably lower toward treeline in the open subarctic spruce-lichen forest.

Fire records for Wood Buffalo National Park, Alberta and N.W.T., for 1952 to 1957 show a total burn of 451 441 ha, or more than 2 percent annually (Kelsall 1968). This suggests a fire cycle close to 50 years for that area, which lies southwest of the areas studied by Johnson and Rowe and by Scotter, and well into the main boreal forest. The Park is characterized by extensive areas of white spruce-aspen "mixwoods," and substantial areas of black spruce and jack pine.

The problem with all of the above studies is that they rely on fire occurrence records over a short time, giving little assurance that they are representative of long-term trends. Scotter (1964) made an analysis of broad forest age classes for an area northeast of Fort Smith, N.W.T., based on successional status of stands (not on actual ages). He concluded that forest burning (mostly lightning-caused) for the period 1944 to 1959 had increased 1.4 times over the period 1885 to 1944 and 3.1 times over the period 1840 to 1844. But his work was based on a map made from small-scale high altitude aerial photographs, and it is doubtful that the classification of stand age groups used was precise enough to allow firm conclusions. Even then, Johnson and Rowe have shown that the rate of burning calculated by Scotter does not exceed 1 percent of the total forest annually--suggesting a 100-year fire cycle.

To avoid these problems, Rowe and others (1974, 1975) have made extensive fire scar and stand age analyses along the Mackenzie Highway and northward down the Mackenzie Valley. These studies provide insights into the variability of fire regimes within a subregion of the boreal forest due to differences in vegetation. To my knowledge such data are not yet available elsewhere in the entire Canadian or Alaskan boreal forest. Three quite different fire regimes were found:

- (1) Flood plain white spruce forests showed the least fire evidence--some stands having escaped fire for 300 years. Sparsely forested rocky uplands were also quite fireproof. Many areas of both types show little evidence of past fires.
- (2) Near Fort Simpson, N.W.T., an extensive area of level to rolling sandy and silty soils supporting stands of jack pine and mixed-woods (pine, spruce, aspen, birch) was sampled. Here a regime of periodic creeping surface fires that often failed to kill all trees was found, with 90 percent of all fires on level plains being surface fires, compared to 64 percent of all fires on rolling topography (out of a total of 73 documented fires). Numerous jack pines bore one or more fire scars. The mean time since the last fire was 30 years for level terrain and 68 years for rolling terrain, for a range of stand ages from 6 to 175 years. The mean interval between fires for both landforms combined was 23 years.
- (3) Near Norman Wells, N.W.T. (Chick Lake Basin), 53 stands of black spruce or black spruce-white spruce mixtures were sampled in a glacial lake basin and adjacent morainic upland. The fire regime was clearly one of medium to long return interval crown fires or severe surface fires that eliminated old stands and created new even-aged forests. The range of stand ages was 0 to 170 years for lake basin sites and 35 to 220 years for morainic uplands. Mean intervals between fires were 83 for lake basin sites and 92 for morainic uplands. Mean time since the last fire averaged 78 years for lake basin sites and 104 years for morainic uplands (here essentially the same as average stand age). The range of intervals between fires was 40 to 170 years for lake basin sites and 35 to 160 for morainic uplands.

These different fire regimes underscore the variability in lightning-fire regimes that can be expected in a large region due to differences in landforms and vegetation.

In their summary, Rowe and others (1974) state that severe fire years throughout the entire Mackenzie Valley are infrequent, although both Fort Simpson and Norman Wells (280 miles [450 km] apart) experienced many fires in 1863 and 1881. High fire years at Fort Simpson were: 1904, 1911, 1929, 1941, 1944 (42 percent of all fires); at Norman Wells: 1863, 1881, 1917, 1969 (60 percent of all fires). The climate that produces fires over the valley therefore often seems to be subregional rather than general. In roughly 1 year out of 4 there are significant fires somewhere in the valley. I must note, however, that 1863 or 1864 have also been identified as high fire years in Jasper Park (Tandé 1976), in the Bitterroot Mountains of Montana (Arno 1976), in the Colorado Rockies (Clements 1910), and in Minnesota (Frissell 1973, Heinselman 1973). Thus, in at least some years, the droughts that produced major fire activity were subcontinental in scale. It should also be noted that 1889 and 1910, both very high fire years in the Rockies, were evidently unimportant in the Mackenzie Valley.

There are no actual fire rotation data for the southern or eastern boreal forest, but extrapolation from the near-boreal Boundary Waters Canoe Area along the Ontario border in Minnesota suggests that even in midcontinent on the southern fringe of the boreal forest, fire regimes were not drastically different from those 1,600 miles (2 575 km) to the northwest. In the BWCA most fires in jack pine, black spruce, or spruce-fir were crown fires or severe surface fires that killed and regenerated stands. The average annual rate of forest burning in presettlement times was about 0.8 percent of the study area (including large areas of nonboreal vegetation). The average interval between fire years was 4.3 years in presettlement times, but most of the ecologically significant fires occurred in just a few major fire years that recurred at intervals averaging 28 years. Many fires in those years were large in area--some in excess of 100,000 acres (40 000 ha). The average fire rotation

for the whole 1,000,000-acre (405 000-ha) study area was about 100 years in presettlement times, based on actual fire-year maps. However, Van Wagner (1978) has shown that my stand origin data from this study indicate a presettlement age class structure due to fire that fits a negative exponential distribution approximating a 50-year fire cycle. The data for the stand origin maps are better than those for the fire-year maps from which my fire rotation estimate was derived, because the fire-year maps suffer from the problem of lost record of overlapping fires in the distant past. Van Wagner's approach may therefore give a better estimate of the fire cycle than mine did. I will discuss this question further in my conclusions to this section of the paper.

In the remaining uncut boreal forest in northwestern Ontario large outbreaks of lightning-caused fires in jack pine and spruce occur every few years (Walker and Stocks 1972; Stocks and Walker 1973; Stocks 1975; Methven, Van Wagner, and Stocks 1975; Donnelly and Harrington 1978). For example, the 9 largest of the Sioux Lookout fires of 1961, all lightning-caused, burned 1,087,350 acres (440 045 ha) of mostly jack pine and spruce, of which more than 654,000 acres (264 670 ha) were classed as "mature" and 340,000 acres (137 596 ha) as "second growth." Aspen and paper birch stands accounted for only some 74,000 acres (29 947 ha). Much of the total run of these fires occurred on July 1, when spread rates of 2 mi/h (3.22 km/h) were sustained from 1:00 to 4:00 p.m. In 1974, Red Lake Fire No. 31 burned some 133,187 acres (53 900 ha) between ignition on June 29 (by lightning) and final control late in July. The most spectacular run occurred on July 13--a run of 10 miles (16 km) from noon to 8:00 p.m. (2.67 km/h). The principal vegetation types burned were jack pine-black spruce mixtures with feather moss ground cover (Pleurozium schreberi and Hylocomium splendens). The areas of both the 1974 Red Lake and 1961 Sioux Lookout fires were typical rolling Canadian Shield terrain, with thin bouldery soil over bedrock, and thick organic layers. The organic layers were almost totally consumed. Revegetation studies in these burns in the fall of 1975 showed that virtually all areas were reproduced to stand mixtures similar to the burned forests (Methven, Van Wagner, and Stocks 1975). All burns contain some skipped areas--an important seed source for some species, but jack pine, black spruce, and aspen require no survivors for their regeneration. Accounts of many similar fires in Ontario could be cited (Leslie 1954, Donnelly and Harrington 1978).

The still unexploited boreal forests of northern Manitoba, Ontario, and Quebec may now have a higher proportion of man-caused vs. lightning-caused fires than do the remote forests of western Canada, simply because of the greater human populations in eastern Canada, and the greater amounts of logging and mining underway in the east (Simard 1975, Stocks and Hartley 1979). But lightning-caused fires are probably still responsible for most of the annual burned area, and the real question is whether man is serving merely as an alternate source of ignition or in some way fundamentally changing the fire regimes. Some lightning-caused fires are also now being suppressed, thus cancelling out some man-caused ignitions. Unless the season of burning or the geographic location of most man-caused fires is quite unnatural, the net effect of the current level of man-caused ignitions and fire suppression in unexploited areas may be small, and there may be little real change in fire frequency, total area of burn, or fire effects. Fire is still the principal agent of forest destruction and renewal in most forest sections, and the vegetation mosaic of most eastern boreal forests is still a complex of even-aged and postfire stands dating closely from past fires. Most fires are crown fires, or severe surface fires, killing and regenerating whole stands, and many fires are very large in area, just as in western Canada (Sharpe and Brodie 1931, Wilton 1964, Wilton and Evans 1974, Simard 1975, Donnelly and Harrington 1978).

The average natural fire cycles for various regions and vegetation types are not well known for the eastern boreal forest, but the even-aged stands of black spruce, jack pine, white spruce, aspen, and balsam fir characteristic of large regions are proof that fire rotations have averaged less than the normal lifespans of these species.

Most jack pine, black spruce, and aspen areas probably have natural fire cycles that average less than 120 years, and many less than 100 years. Some areas dominated by balsam and white spruce may have longer fire cycles, but we do not really know how long. Creeping surface fires that fail to kill much of the stand do occur in some jack pine and aspen-birch areas, but this is not a dominant fire pattern.

In the large areas of eastern boreal forest now being exploited for pulpwood, fire protection levels are much higher, but logging slash creates extreme hazards, and many wildfires still occur. Natural fire cycles and natural regeneration patterns are much changed in such regions (Donnelly and Harrington 1978, Harrington and Donnelly 1978, Stocks and Hartley 1979). A method of calculating the proper allowance for unavoidable wildfire in exploited forests has been proposed by Van Wagner (1978).

ALASKAN AND WESTERN YUKON DIVISION OF BOREAL REGION

Interior Alaska and the Dawson Section (B.26a) of the Yukon are characterized by vast white spruce-birch and aspen forests on the more productive sites, and extensive stunted black spruce forests on north slopes, seepages, and lowlands. This region contains the highest mountain ranges in North America: the Alaska Range where Mt. McKinley reaches 20,300 ft (6 189 m) and the Wrangell-St. Elias Range where Mt. Logan reaches 19,850 ft (6 052 m). Alaska is rimmed on the north by the Brooks Range.

Alaska's northern location and mix of high mountains and major lowlands creates a complex of moderately productive spruce-birch-aspen forests in the lowlands and river valleys, and open subarctic spruce-lichen woodlands on the lower mountain slopes--much of the latter transitional to either true arctic tundra or low altitude "alpine" tundra (the treeline of most interior mountains is near 3,000 ft [915 m]) (Viereck 1973).

Most interior Alaska forest fires are relatively high intensity crown fires or severe surface fires that kill and regenerate entire stands. This is particularly true of closed white spruce or black spruce forest. Fire years are sporadic in occurrence, and most of the area burned occurs in just a few major fire years, but such years tend to occur at least once every decade. For example, for the 30 years 1940 through 1969, Barney (1971) reports that the total area burned in interior Alaska was 29,461,711 acres (11 922 991 ha) or an annual average of 982,057 acres (397 433 ha). However, much of this acreage actually burned in just 3 major fire years: 1940, 1957, and 1969--when more than 4 million acres (1.6 million ha) burned each year. There is much evidence that similar rates of burning have occurred far back into the past (Lutz 1956, 1963; Viereck 1973). Lutz estimates the annual rate of forest burning in the early settlement era to have been 1,000,000 acres (405 000 ha) per year, but Barney (1971) believes the true rate to have been 1.5 to 2.5 million acres (0.6 to 1.0 million ha) per year. That would indicate a fire cycle of about 110 years in the gold rush days. Unfortunately, all of these estimates apparently include much tundra as well as forest. Taking the actual record for the 20 years 1950 through 1969, for which vegetation type breakdowns are available (Barney 1971), the annual rate of burning for forested land for interior Alaska's 118 million acres (48 million ha) of forest is about 446,000 acres (180 494 ha) or 0.38 percent--giving a present fire cycle of 265 years. If Viereck's (1973) gross burnable area figures are used with Barney's total burn area data, the fire cycle is 147 years. The actual fire cycle may be shorter than either of these estimates indicate, but no better published data are available.

Of 6,101 Alaska fires recorded from 1950 through 1969, 70.5 percent were man-caused, and 29.5 percent were lightning-caused (Barney 1971). But lightning-caused fires still burned 78 percent of the area consumed by fires for which such records are available (1950-1969). This is so because lightning fires occur at random all over

the interior, including many remote areas where control is difficult and costly and no property values are threatened. Such fires are given low priority when fire workloads exceed control capabilities. In contrast, most man-caused fires are in accessible areas, and many do threaten significant values. The peak month for man-caused fires is May, while lightning fires peak in June. Lightning fires have been reported from May through September, (Requa 1964). Many fires in remote areas are very large in area--some covering hundreds of thousands of hectares. Most of the area burned in any decade is the result of these large fires. This is true in the Dawson Section of the Yukon as well as for interior Alaska.

Little of interior Alaska's potentially exploitable forest has yet been logged, and the same is true in the Yukon. Where such forests are being cut, the fire situation is quite different from that just reviewed. Hazard is at a peak when slash is fresh during the first few years after cutting, and most exploited areas are given some fire protection. Thus the fire regimes of such areas are greatly altered from those of unexploited regions. No estimates of fire cycles for such forests are available. Regeneration there hinges heavily on man's actions, and a major question is whether the occurrence of some wildfire is being allowed for, since total fire exclusion is unlikely even in intensively managed forests (Zasada 1971).

CORDILLERAN AND FOOTHILLS DIVISIONS OF BOREAL FORESTS

This region includes Rowe's B.19, 24, 25, and 26 Sections (except 26a)--portions of the boreal forest occupying the foothills and outliers of the Rocky Mountains with significant Cordilleran floral elements. Here the lodgepole pine, Engelmann spruce, and subalpine fir often play the same ecological roles as do jack pine, white spruce, and balsam fir in the main boreal region. White spruce is also common, however, and there are many areas with extensive hybridization between the Engelmann and white spruces. Black spruce, quaking aspen, and paper birch occur throughout--the black spruce forming a common postfire type on peatlands, north slopes, and other cold, wet sites.

Again, the dominant fire regime is one of short to moderately long return interval crown fires or severe surface fires that kill most trees and regenerate large areas to new even-aged forests. Because of the rolling to mountainous relief of much of this Division, topography plays a stronger role in controlling fire movements and ultimate fire size than in much of the main boreal forest. Many fires are large, covering whole watersheds or running up mountainsides nearly to timberline. Typical maximum fire size may be slightly lower than in the main boreal division because of the greater landform diversity of the Cordilleran foothills. Creeping surface fires do occur in some lodgepole pine stands, but typically burns are severe enough to kill most trees.

Some estimates of fire cycles are now available for parts of Northern British Columbia based on forest inventory stand age data (Smith 1980). Van Wagner (1978) has estimated that presuppression fire cycles in the southeastern fringe of the area were about 50 years for lodgepole pine forests, and have now lengthened to 65 years or more with some fire control. Lightning-caused fires are common, and probably account for most of the burned area in the more remote regions. According to Requa (1964), 76 percent of all fires in the Yukon were lightning-caused. Man-caused fires are also of major importance in the more developed regions, an example being the massive fires of 1968 in west-central Alberta--some within this Division (Kiil and Grigel 1968). Logging is now extensive in a few southern areas, and land clearing is also occurring in some areas. In such areas the natural fire cycle is probably much altered by both man-caused ignitions and changes in fuels due to logging. Fire control has also recently become quite effective in certain areas. There is reason to believe that presettlement fire cycles would be similar to that documented for Jasper Park by Tande (1976) and to the cycles estimated for interior Alaska.

Aspen Parkland

In western Canada Rowe's B.16 (Aspen-Oak) and B.17 (Aspen Grove) sections are so different in vegetation and fire history from the remainder of the Boreal Region that they require separate treatment. In presettlement times both sections marked an ecotone between prairie and northern forest, with quaking aspen the principal tree. Apparently this ecotone was maintained in a savanna-like condition by short return interval prairie fires that burned into the aspen forest, killing back young trees and maintaining large sections in true prairie (Ewing 1924, Buell and Buell 1959, Bird 1961, Buell and Facey 1960, Heinselman 1974).

Fire frequency in presettlement times is not well known, but there must have been fires every few years--perhaps at return intervals of 2 to 15 years. Many of those fires may have been set by Indians either deliberately or accidentally, since the adjacent plains had significant Indian populations over long time periods. Fire intensity was probably low, but varying somewhat with return interval and age of the forest and shrub patches burned. Small diameter aspen stems are easily killed with moderately intense grass fires, and the open condition of much of the land suggests that most fires did return frequently enough to keep the aspen young and vulnerable. Since aspen suckers quickly form underground roots, most aspen patches would persist unless burned repeatedly and intensely at very short intervals. In presettlement times as one progressed from the open prairie northward into this region there must have been a gradual increase in size or abundance of forest patches and a concomitant decrease in fire frequency, until ultimately the closed aspen-birch-spruce forests of the full boreal forest were reached.

Today agriculture and fire suppression have vastly changed this ecotone, but even now bits of natural savanna remain, and the region still bears the stamp of its early history. Much land is cultivated, and fire suppression has allowed many aspen patches to mature. Some aspen stands have apparently also now invaded former prairie (Buell and Buell 1959).

Great Lakes-St. Lawrence Acadian Forests

This complex region contains several distinct ecosystems and a strong east to west gradient in fire climate. Local landform and vegetation factors also create different fire regimes within small subregions. Discussion of presettlement fire regimes for the region as a whole would therefore mask important differences, and I will instead discuss vegetation units that had distinct fire regimes before modern man altered the system.

"NEAR BOREAL" CONIFER FORESTS

In northern Minnesota, Wisconsin, and Michigan, southern Ontario and Quebec, and parts of Maine, New Brunswick, and Nova Scotia, there were at the time of settlement substantial areas dominated by the "boreal conifers"--jack pine, white spruce, black spruce, tamarack and balsam fir. Some of these areas supported vegetation intergrading with the red pine-white pine or aspen-birch conifer forests to be discussed below, but I am here discussing the areas with a near-boreal vegetation.

Most such forests apparently had short return interval crown fire and/or severe surface fire regimes, with fire cycles in the 50- to 100-year range. The ecologically significant fires were mostly large or very large from 1,000 to 10,000 acres (400 to 4 000 ha) or more, creating sizeable areas of even-aged forest similar to those in the full boreal region. Most burns probably occurred during severe droughts that tend to recur regionally at 20- to 30-year intervals.

Such a fire regime has been documented for the boreal vegetation types of the Boundary Waters Canoe Area Wilderness in northeastern Minnesota. It is based on stand age and fire scar analyses and actual stand origin maps for nearly half a million acres (168 000 ha) of virgin forest, much of which still dates from fires in the presettlement or early settlement periods, before fire control existed (Heinselman 1973). The full study area consisted of a million-acre (405 000-ha) unit for which 1948 vegetation maps were available based on prelogging aerial photographs. Fuel and weather conditions in the BWCA that can lead to crowning and long distance spread by spotting have been identified by Roussopoulos (1978).

My fire-year maps for the whole study area suggest an approximate 100-year fire rotation for the whole ecosystem, but the boreal jack pine, black spruce, and spruce-fir forests clearly had shorter cycles. Furthermore, Van Wagner (1978) has shown that my own stand origin maps for the 415,000 acres (168 000 ha) of remaining virgin forests document a 50-year fire cycle in presettlement times, if his assumption that my stand age data fit the negative exponential distribution is valid. For this distribution to apply, one must assume that flammability does not increase significantly with stand age. This assumption may not be tenable for many BWCA vegetation types, but it certainly comes closest for the boreal conifer forests, and much of the present virgin area on which Van Wagner based his calculations does support a "near boreal" vegetation. The fact that young jack pine and black spruce stands often do burn in the same fires that consume older forests also supports Van Wagner's analysis. In the BWCA, jack pine and black spruce bear closed or semiclosed cones by age 15 to 20 years, so they are fully capable of stand renewal on very short cycles. The red and white pine forests of the BWCA clearly had different fire regimes, as did some other types. But such forests comprised only a small percentage of the remaining virgin areas, and I am inclined to accept Van Wagner's 50-year fire cycle as approximately correct for the presettlement fire rotation of the BWCA's boreal forests. My stand origin data do fit the negative exponential distribution quite well.

Some of the difference between my 100-year rotation based on fire-year maps and Van Wagner's 50-year cycle is probably due to loss of record of earlier fires through the effects of later overlapping burns. The remainder of the difference may be due to the selective elimination of older forests by logging during the interval 1948 to 1972. This undoubtedly made the forest age structure of the full 1-million-acre (405 000-ha) study area that my estimates are based on somewhat different from that of the remaining 415,000 acres (168 000 ha) of virgin forest upon which Van Wagner's estimate is based.

Farther south, on the xeric glacial outwash sand plains of central Wisconsin and lower Michigan and in other southerly xeric sites, many jack pine areas apparently had regimes of short return interval moderate intensity surface fires that killed out only portions of stands. Such regimes created the open, patchy, multiaged pine stands that characterized these "pine barrens" in presettlement time (Marschner 1930, Heinselman 1974). We lack good estimates of the primeval fire cycles for such areas (see Curtis 1957, Vogl 1970). However, Vogl's (1970) work and comparisons with the crown fire regime of the BWCA and with the surface fire regimes of jack pine in the N.W.T. suggests average return intervals for individual stands in the 15- to 35-year range. It is noteworthy that much of the jack pine in those areas has nonserotinous (open) cones--probably a genetic adaptation to the prevailing fire regime (Rudolph and others 1959). Some areas that are jack pine savannas today were productive red pine or white pine forests prior to the logging era and subsequent slash fires. The areas described here were original jack pine barrens.

Farther east, in eastern Ontario, Quebec, New Brunswick, Nova Scotia, and Maine there were also many outliers of boreal vegetation within the Great Lakes-St. Lawrence and Acadian Forests. Jack pine was less common and balsam fir more abundant. There is reason to believe that the length of fire cycles increased eastward in response to the precipitation gradient, but even in southeastern Canada and Maine severe droughts

do occur at long intervals, and major fire episodes are possible (Strang 1978). The Miramichi Fire of 1825 in New Brunswick and Maine burned over some 20,000 square kilometers (almost 5 million acres)--the largest forest fire ever recorded in North America (Wein and Moore 1977). Some of that fire burned in boreal vegetation, although large-scale logging and land clearing in other vegetation types were its principal causes. In presettlement times the ecologically significant fires in the boreal vegetation of these eastern regions were probably large to very large high intensity crown fires or severe surface fires at long return intervals. Fire rotations probably averaged 100 years or more. Significant Indian populations were present before European colonization began, and man may have been a larger contributor of fires here than in the full boreal forest (Day 1953). Lightning ignition frequencies are low (Wein and Moore 1977), but lightning could still cause large-scale crown fire episodes at long intervals.

The larger peatlands and smaller bogs and swamps of the northern Lake States, eastern Canada, and Maine also support an essentially boreal vegetation, but their fire regimes were often different from the regimes of mineral soil areas. The principal trees of these wetlands are black spruce, tamarack, and northern white-cedar, and the undervegetation is a complex of northern ericaceous shrubs, mosses, lichens, and a few herbs and sedges. Some large peatlands, especially in Minnesota, are really fens and support great expanses of sedges and grasses (Heinselman 1963).

Forested peatlands with a moss ground layer will not carry spring fires readily because their water tables are too high in spring due to snowmelt recharge--even in the driest seasons, and there is no highly flammable field layer of dried grasses and sedges to carry surface fires. In contrast, sedge and grass fens, even those with partial tree cover, burn best in spring because the dried grasses and sedges carry fire very well, sometimes even over water, and in summer the new growth is too succulent to carry fire. Thus, most fires in forested peatlands occur in July, August, or September of severe drought years--when water tables are low enough so that moss layers become thoroughly dessicated. Under these circumstances, given sufficient wind, the spruce, tamarack, and cedar forests of these wetlands can carry major crown fires. Most fires in sedge-grass fenlands occur in April, May, or early June before significant new growth of sedges and grasses has occurred.

The presettlement fire regime for large forested spruce bogs in Minnesota was apparently one of long return interval crown fires, often of large size, with fire cycles of perhaps 100 to 150 years. I base this estimate on much stand age work and study of charcoal layers in black spruce bogs throughout northern Minnesota (Heinselman 1963, 1970). In the BWCA many black spruce bogs did burn in the same crown fires that killed and regenerated the surrounding jack pine-black spruce forests on mineral soils, but some were skipped by many fires, and their average fire cycles are longer than for upland forests. The vast grass-sedge fens of north-central and northwestern Minnesota burned much more frequently. Most fires were probably set by man in the spring. The presettlement fire regime was probably one of periodic surface fires at fire cycles of 5 to 30 years.

RED PINE-WHITE PINE FORESTS

The famous "pineries" of Michigan, Wisconsin, and Minnesota, and of southern Ontario, Quebec, New Brunswick, and Maine depended on fire for stand establishment, and on many sites also for the control of understory competition and fuel buildup. There was probably more fire in these ecosystems in the west than near the east coast, but the only detailed studies of fire cycles come from three western areas: Itasca Park, Minnesota (Spurr 1954, Frissell 1973), Algonquin Park, Ontario (Cwynar 1976) and the BWCA (Heinselman 1973).

My own studies in the BWCA document a presettlement fire regime in most red and white pine stands of infrequent moderate surface fires, with an average return interval of 36 years, punctuated at much longer intervals--perhaps 160 years--by severe surface fires or crown fires that killed portions of stands and brought in new age classes. Other stands escaped scarring fires, but were clearly of postfire origin. Since red and white pine do not have persistent or serotinous cones, and only infrequent good seed years, there must be survivors to reseed the burn unless the fire happened to occur in the fall of a good seed year. Significant red and white pine stands do not become established beneath a forest canopy in the BWCA, so a major disturbance was essential for stand establishment. Fire scar dates, stand ages, and charcoal evidence indicate that fire was the factor that accounts for stand establishment in virtually all cases. It is less clear that periodic surface fires were essential, but in some stands such fires occasionally scarred trees at intervals as short as 5 years.

At Itasca Park Frissell (1973) found similar fire evidence, fire regimes, and stand responses in red and white pine, but his average return interval for surface fires scarring individual trees was 23 years, with a range of 13 to 38 years. Except for somewhat more frequent fires in the settlement period, the Itasca record is similar to that for the BWCA. Many of the Itasca pine stands were relatively pure red and white pine mixtures until fire exclusion in the last 60 years encouraged the invasion of balsam fir and sugar maple understories.

Farther east less detail on fire cycles is available, but Cwynar's (1977) fire scar work in Algonquin Park, Ontario, suggests fire regimes basically similar to those in Minnesota. Maissurow (1935, 1941) and Cary (1948) long ago recognized the importance of fire in establishing white pine stands in Wisconsin, Michigan, and New England. A careful reconstruction of the history of a single plot in former white pine forest in New Hampshire showed that fire directly preceded stand establishment in about 1665 at that site (Henry and Swan 1974).

Throughout the region, from Maine to Minnesota, there were really two classes of pine forests from the standpoint of fire regimes: (1) The classic pure red pine-white pine groves, with little understory development, and almost no mixture with shade tolerant conifers or hardwoods. Such forests probably had a history of periodic light surface fires at 5- to 50-year intervals, in addition to severe fires at longer intervals that brought in whole new age classes of pine. These kinds of stands generally grew on the more xeric sites or in more fire-prone physiographic situations. Much of Kuchler's (1966) Type 86--Great Lakes Pine Forest--belonged to this class. (2) White pine forests (usually with less red pine in mixture) with significant stand components of shade-tolerant conifers or hardwoods--such as eastern hemlock, white or red spruce, balsam fir, northern white-cedar, sugar maple, beech, yellow birch, red maple, or similar species. This class of stands occurred on more mesic sites or perhaps also on sites better protected by their physiographic location from periodic surface fires. Such stands were probably more common from Michigan eastward due to heavier precipitation, while the first class was probably more common in the drier climates of Wisconsin, Minnesota, and western Ontario. The second class of stands apparently had a history of only one severe fire at very long intervals, which killed most of the previous generation and brought in a whole new forest. Fire cycles for forests of this type may have averaged 150 to 300 years.

Paleoecological studies based on charcoal and pollen frequencies in laminated lake sediments show that white and red (or jack) pines have been associated with fire ever since their postglacial arrival within their present ranges some 1,000 to 9,000 years ago (Swain 1973, 1978; Cwynar 1978). Fire frequency and intensity have varied with fluctuations in climate and in the abundance of these pines and their hardwood competitors, and fir frequencies at least as high as those documented by fire scars on living trees occurred long before European man reached North America. Thus we must

accept and understand the role of fire in producing the primeval landscapes of the Great Lakes-St. Lawrence region (Wright 1974, Wright and Heinselman 1973). In Minnesota white pine may have reached its present western limits within the last 1,000 years (Jacobsen 1975).

ASPEN-BIRCH-CONIFER FORESTS

The aspen-birch forests of Minnesota, Wisconsin, Michigan, and southern Ontario were also a prominent element in the fire-dependent vegetation of the Great Lakes-St. Lawrence region. One might conclude from the early ecological literature and from Kuchler's (1966) map that these forests are an artifact of the destructive logging era around the turn of the century. Actually, aspen and birch were greatly increased in that era, but the presettlement forests also contained a large aspen-birch element.

Marschner's map of the original vegetation of Minnesota (Marschner 1930, Heinselman 1974) recognizes two classes of aspen-birch forests: Aspen-Birch-Conifer Forests and Aspen-Birch-Hardwood Forests. His map was based on the U.S. General Land Office Survey notes for surveys conducted prior to settlement. The Aspen-Birch-Conifer Forests occur in the north, while the Aspen-Birch-Hardwood Forests are in central Minnesota. Marschner understood the successional status of these forests and noted that they would "eventually become" conifer or hardwood forests depending upon the other species that occurred in mixture with aspen and birch. "Aspen-birch conifer forests" of the kinds mapped by Marschner still exist in the some 1 million acres (405 000 ha) of virgin forest remaining in the BWCA Wilderness of northeastern Minnesota and adjacent Quetico Provincial Park in Ontario.

The "aspen-birch conifer forests" of Marschner were simply enclaves of aspen-birch forest with significant coniferous stand elements that merged with nearby forests of red and white pine, jack pine, white and black spruce, balsam fir, and northern white-cedar. In the BWCA their fire regimes were similar to those of adjacent conifer forests. Severe surface fires or even crown fires (in their coniferous components) evidently swept these forests intermittently--with fire cycles of perhaps 80 years. Nearly complete stand destruction was necessary to regenerate their aspen and birch component and bring in a new even-aged stand similar to the previous generation. Sufficient time had to elapse from the previous burn to develop enough coniferous fuels to sustain a hot fire, or else the aspen-birch areas might be skipped by larger scale fires involving many vegetation types. Some skipping of aspen-birch types does seem to occur, and they probably had longer average fire cycles than nearby conifer forests. They also certainly had fewer light surface fires than red and white pine stands.

NORTHERN HARDWOOD-PINE-SPRUCE-FIR FORESTS

This complex of forests had a more southerly distribution within the Great Lakes-St. Lawrence forests than did the previous three types. Kuchler (1966) maps such areas as Northern Hardwoods-Fir Forest (Type 98), Northern Hardwoods-Spruce Forest (Type 99), or Northern Hardwoods (Type 97). I am lumping here all of the forests that consisted of mixtures of sugar maple, yellow birch, beech, white ash, oak, basswood, and any combination of the following conifers: white pine, hemlock, white and red spruce, balsam fir, and northern white-cedar. These forests were complex, and still other species were involved in certain regions.

The available evidence, and there is not much, suggests that such forests often had a semi-even-aged structure, and that their less shade tolerant components were maintained by long return interval disturbance episodes--some of which involved fire. Species that are hard to account for without fire are white pine, yellow birch, red oak, and black cherry (*Prunus serotina*). How severe these fires were, or what the fire cycle may have been we may never know. The work of Stearns (1949) and Henry

and Swan (1974) give the best basis for a judgment. Probably fire was important in maintaining the original species composition and character of these forests, and most fires were severe surface fires that occurred only after prolonged drought--and then touched largely forest that were breaking up due to wind or icestorm damage, insect attacks, and similar events that generate ground fuels. The fire cycle for such forests must have been erratic, but intervals of 200 to 300 years between fire episodes are plausible.

NORTHERN HARDWOODS FOREST

Toward the southern fringes of my region there apparently were some hardwood forests essentially lacking any conifer component. These forests were dominated by oaks, sugar maple, basswood, yellow birch, red maple, white ash, American elm, beech, and other species. Again the question: Did fire play a significant role in the life cycle of such forests? Some species, such as certain oaks, yellow birch, black cherry, and perhaps basswood seem to require disturbance to account for their presence. Windstorms were certainly a factor, but perhaps fires were also important. Spring and fall fires in years of extreme drought are clearly possible in such forests--and windstorms or other causes of stand breakup could add enough heavy fuel to create fires with the potential to alter the ecosystem significantly. We have no reliable information on the past extent or timing of such fires, but they probably did occur. Farther south in the Appalachian Mountains, Barden and Woods (1973) have documented lightning-caused fires in hardwood forests not greatly different from those in question. May was the peak month for lightning fires.

ASPEN-BIRCH HARDWOOD FORESTS

Marschner (1930) mapped substantial areas in east-central Minnesota as forests of quaking and bigtooth aspen (Populus gradidentata) mixed with paper birch, sugar maple, oaks, basswood, elm, and other hardwoods. They were clearly postfire successional forests, and give credence to the idea that, at least in Minnesota, hardwood forests lacking conifers did burn. We have little basis for speculating about the character or frequency of such fires, but they must have been common. Perhaps many were deliberately set by the Indians in the spring or fall--the only seasons when such forests will burn. Some of these aspen-birch-hardwood forests may have been the early post-fire stages of fires that had burned older northern hardwood forests containing little aspen and birch.

THE IMPACT OF LOGGING, SETTLEMENT, AND FIRE CONTROL

The Great Lakes-St. Lawrence and Acadian Forests have been altered much more by European man than have those of the full Canadian and Alaskan Boreal Forests or the Subalpine Forests of the Rocky Mountains. The first settlements were in Massachusetts in the early 1600's. Settlement gradually spread westward and northward, reaching northeastern Minnesota and adjoining areas in Ontario about 1875. Many areas in New England, New York, Massachusetts, and Pennsylvania were cleared for agriculture by 1800. Some of the best lands in the valleys and flatlands are still cultivated, but most of the steeper, rockier lands were abandoned during the 1800's, as the better agricultural areas of the midwest and plains were developed (see Lull 1968). In Maine, Nova Scotia, New Brunswick, Quebec, and eastern Ontario land clearing began in the 1700's, but it proceeded at a slower pace, and most of the forest never has been cleared to the present time. The forest is now broken up by cultivated lands and pastures in many areas, however--substantially changing the potential for fire movements.

In northern Michigan, Wisconsin, Minnesota, and western Ontario land clearing and farming did not arrive until the big pine logging era began--in the early 1800's in Lower Michigan, but not until 1870 or later in many western and northern regions.

Varying percentages of the land were ultimately cleared for agriculture in the northern forests of these States, but a period of land abandonment began with the depression of the 1930's, and most of the poorer sandy soils and steep or rocky fields have now reverted to forest or brushlands. Again, many forest areas are now broken up by scattered tracts of cultivated land, and in the southern forest regions and better soil areas the present landscape is a patchwork of forest and agricultural lands (see Merz 1978).

The big pine logging era had the greatest impact of any events in the last several centuries on the presettlement ecosystem and fire regimes of this entire region. Logging for white and red pine sawtimber began in Maine on a large scale in the early 1800's, and progressed rapidly westward through New York, southern Quebec, Pennsylvania, and eastern Ontario, reaching Lower Michigan on a large scale just after the Civil War. Minnesota was the final stand of the white pine industry, and most of its virgin pine forests were gone by the beginning of the Great Depression in 1929. Nearly all of the merchantable pine in the entire region was thus logged off in about a century (Larson 1949). Settlers moved into many areas as the logging progressed, and most people had little regard for the forest because it was expected that most areas would be cleared for agriculture. Fires were routinely used in land clearing, and most cutover areas eventually burned several times--especially in the Lake States, where forest destruction was the greatest.

Then came the great disaster fires: 1825--the Miramichi in New Brunswick and Maine--5 million acres (2 million ha); 1871--the Peshtigo, Wisconsin--1,280,000 acres (518 000 ha) and the Lower Michigan--2,500,000 acres (1 million ha); 1881--the Thumb, Lower Michigan--1 million acres (405 000 ha); 1894--the Hinckley, Minnesota--160,000 acres (65 000 ha); 1910--the Baudette, Minnesota--300,000 acres (121 000 ha); 1918--the Cloquet-Moose Lake, Minnesota--1,280,000 acres (518 000 ha). Even worse, some 2,700 people perished in these fires. All of these disaster fires burned in the fall, most in September or October after a long period of drought, and on days with clear skies, high temperatures, low humidities, and high winds. All were fueled by combinations of logging slash (much of it pine), land clearing debris, cured hay lands and pastures, and patches of uncut timber--much of it coniferous (see Haines and Sando 1969, Holbrook 1960, Wein and Moore 1977).

These conflagrations, plus the countless settler fires that burned and reburned the cutover lands for decades, finally reduced the presettlement forest ecosystems of this vast region to a shadow of the original (Larson 1949, Zasda, Heinselman and Voigt 1954, Holbrook 1960, Shands and Healy 1977). It was not the fires alone that accomplished the changes in forest composition and structure, but rather the combination of logging, slash-burning, and land clearing, and repeated fires at short intervals on the old cutovers. These human activities together reduced or eliminated the seed sources for most of the conifers, and killed back many hardwood stands to the point where only sprout growth could replace them. In Minnesota, Wisconsin, and Michigan alone some 5 to 6 million acres (2 to 2.4 million ha) of white and red pine forest were converted to essentially pure aspen and birch stands--almost totally devoid of pine seed trees (Heinselman 1954). This was possible despite the natural adaptations of these pines to fire, because logging directly removed most seed trees, and left what few remained in an altered fuels situation where subsequent hot slash fires could readily kill them.

If logging alone had occurred, in some cases regeneration to the pines and other conifers might have been complete due to advance growth already present, or from seeds shed during the logging process. But even one severe slash fire greatly reduced the chances of successful regeneration of the pines and most other conifers. Jack pine

and black spruce were exceptions--their closed cones often supplied enough seed to regenerate them if they were left standing after the logging. The effects of these varied postlogging fire regimes can still be seen in the BWCA in the areas logged for white and red pine between 1895 and 1930 (Heinselman 1969, 1973). Where logging left adequate seed sources and the slash fires were not too intense, good pine regeneration sometimes resulted (Burgess and Methven 1977).

The increase in fire frequency during the early logging and settlement era also touched those few areas within the region that were ultimately to escape the direct impact of logging. Fire history studies in the unlogged portions of Itasca State Park (Frissell 1973), the BWCA (Heinselman 1973), and Isle Royale National Park (Hansen, Krefting, and Kurmis 1973) all show an increase in fire frequency for that era. But in most cases these changes only resulted in a 30- to 50-year period of shorter fire cycles. Many stands were not affected, and those that were simply were visited earlier or more frequently by fire than they would have been if the presettlement regime had continued. The effect on the ecosystem was not major, and can still be reconstructed. Seed sources for the red and white pines were not lost in most areas.

A general awakening to the need for forest conservation developed in North America early in the present century. By 1925, fire prevention and control programs were becoming well organized in most of the Great Lakes-St. Lawrence and Acadian forest region. There was little recognition of the possible natural or beneficial roles of fire, and total fire exclusion became the goal of the new State, Provincial, and Federal forestry departments. While that goal has still not been achieved, the era since 1925 has seen a complete reversal of fire regimes, to the point where for most vegetation types, fire during the life of existing stands has become a very improbable event. For example, Wein and Moore (1977) estimate that the mean fire rotation for New Brunswick forests for the period 1931 to 1975 was about 1,000 years, with a range of 230 years for the red spruce-hemlock-pine type in the northeast, to more than 5,000 years for many other vegetation types. Most of the fires that did occur burned in slash areas produced by pulpwood logging. In the developed forest regions of southeastern, south-central, and southwestern Ontario fires have burned only a tiny fraction of the area in recent decades (Donnelly and Harrington 1978). For the 10 National Forests in the Lake States and the Northeast, the average annual burn from 1960 to 1969 was 0.016 percent, or a fire rotation of 6,301 years! That figure is for a total protected area of 11,594,000 acres (4 692 000 ha) (Haines, Johnson, and Main 1975). Statewide figures for the same region would yield a somewhat shorter fire rotation, but for this entire region fire rotations for most vegetation types in most areas are now in excess of 1,000 years. This compares with presettlement regimes of 50 to 300 years for the various types.

SUMMARY AND DISCUSSION OF FIRE REGIMES

Table 1 summarizes the presettlement and present fire regimes for most of the northern ecosystems discussed in this paper. The estimates of fire cycles are my own, but where they are based on substantial evidence in the literature, the principal source reference is given. In a few cases these sources actually made direct estimates of fire cycles, and those are reported where applicable, but most authors have not reduced their evidence to fire cycle estimates and I have attempted to fill that gap. Most of these fire cycle estimates are at best crude approximations. They are put forward in an effort to quantify the differences between ecosystems, and to challenge future investigators to refine them.

TABLE 1.--Presettlement and modern fire regimes for selected northern ecosystems

Forest region, location, ecosystem type	Approximate presettlement fire regime			Source	Approximate present fire cycle
	Fire regime type ^{1/}	Typical fire size ^{2/}	Fire cycle		
		Years	Years		
ARCTIC-ALPINE TUNDRA					
Canadian Arctic Islands	0	--	--	Wein 1976	--
Canadian and Alaskan Trunda near treeline	1	small	500?	Wein 1976	500
Alpine Tundra-Rocky Mts., W.U.S., Canada	1	small	300?	Habeck and Mutch 1973	1000+
Alpine Tundra-New England	0	--	1000+	Estimated	1000+
SUBALPINE FOREST					
S.A.1 Lodgepole P.--lower elevations	2-3	medium	25	Tande 1977	1000+
S.A.1 Lodgepole P.--midelevations	3-4	large	50	Tande 1977	1000+
S.A.1 Spruce-Fir-Lodgepole P.--higher elevations	4	medium	100	Tande 1977	1000+
S.A.1 Lodgepole P.-Spruce Fir	3-4	large	55	Day 1972	450
Bob Marshall Wilderness, Mont.:					
Lodgepole P.--lower elevations	5/2	medium	150/125	Gabriel 1976	1000+
Lodgepole P.--midelevations	5	large	150	Gabriel 1976	1000+
Spruce-Fir--higher elevations	6	medium	300+	Gabriel 1976	1000+
Bitterroot Mountains, Mont.:					
Lodgepole P.--midelevations	1-4	large	25	Arno 1976	1000+
Lodgepole P.-Fir--higher elevations	5/3	medium	150/35	Arno 1976	1000+
Yellowstone-Grand Teton Natl. Parks, Wyo.:					
Lodgepole P.--lower elevations	2-3	medium	25	Houston 1973	1000+
Lodgepole P.--midelevations	3-4	large	75?	Loope, Gruell 1973	1000+
Spruce-Fir-Lodgepole P.--higher elevations	5	medium	150?	Loope, Gruell 1973	1000+
Lodgepole P.--Colorado Rockies	4	large?	100?	Clements 1910	1000+
Quaking Aspen--Colorado Rockies	3	large?	100?	Estimated	1000+
Balsam Fir-Red Spruce--New England Mts.	0	--	1000+	Estimated	1000+
BOREAL FOREST					
Interior Alaska--N.W. Yukon:					
Open Spruce-Lichen Forest	5	large	130	Viereck 1973, Barney 1971	200
Closed Spruce-Birch or Black Spruce	4	very large	100	Viereck 1973, Barney 1971	150
Floodplain White Spruce	6	small	200+	Viereck 1973, Barney 1971	500+
N.W.T.--Mackenzie:					
B.27 Open Spruce near treeline	5	medium	120	Johnson and Rowe 1977	120
B.23a Norman Wells-Black and White Spruce	4	very large	100	Rowe and others 1974	100
B.23a Fort Simpson--open Jack Pine	4/3	large	100/25	Rowe and others 1974	100/25
B.23a Floodplain White Spruce	5	small	200+	Rowe and others 1974	200+

N.E. British Columbia:					
B.19b Lodgepole P.	4	large	49	Smith 1979	202
B.24 Spruce	5	large	103	Smith 1979	202
North Alberta--Wood Buffalo Natl. Park:					
B.23a, B.18b Mixed Woods	4	large	50	Estimated	50
West Alberta--B.19c Lodgepole P.-Spruce	4	large	50	Van Wagner 1978	90?
N.W. Ontario--B.22a Jack Pine-Black Spruce	4	very large	60	Estimated	90?
N.W. Ontario--B.4 Black Spruce	4	large	100	Estimated	?
Hudson Bay Lowlands--B.5 Black Spruce	5	large	150	Estimated	150
Quebec--B.1b Black Spruce-Jack Pine	4	large	100	Estimated	?
Quebec--B.13a Open Black Spruce	5	large	150	Estimated	150
Newfoundland--B.28 Black Spruce-Fir	5	medium?	150	Estimated	?
ASPEN PARKLAND					
Minn., Man., Sask., Alta.	2	large	10	Estimated	1000+
GREAT LAKES-St. LAWRENCE FOREST					
Boundary Waters Canoe Area, Minn.:					
Jack Pine-Black Spruce	4	very large	50	Heinselman 1973, revised	500?
Aspen-Birch-Fir	4	very large	80	Heinselman 1973, revised	2000
Red-White Pines	5/1	medium	180/36	Heinselman 1973, revised	2000
Lake Agassiz Peatlands, Minn.:					
Black Spruce	5	large	150	Estimated	1000+
Itasca State Park, Minn.:					
Red-White Pines	5/2	large	150/20	Frissell 1973	1000+
Harvard Tract, N.H.:					
White Pine-Hemlock-Hardwoods	5	medium?	250	Henry and Swan 1974	1000+
North Wisconsin--Upper Michigan:					
Sugar Maple-Yellow Birch-Hemlock-White Pine	6	large	350	Stearns 1949	1000+
Central Wisconsin--Lower Michigan:					
Jack Pine Barrens	4/2	medium	60/15	Estimated	500+
ACADIAN FOREST					
New Brunswick:					
Red Spruce-Hemlock-Pine	5	large	150?	Wein and Moore 1977	230
Sugar Maple-Hemlock-Pine	5	large	300?	Wein and Moore 1977	1800

1/ For definitions of fire regime types see earlier text discussion, page 13.

2/ Fire size classes are: small=100 acres or less; medium=101 to 1,000 acres; large=1,001 to 10,000 acres; very large=over 10,000 acres.

To make no mistake about the meaning of these numbers, let me repeat my definition of a "fire rotation" (Heinselman 1973), or of Van Wagner's (1978) equivalent term "fire cycle": The fire rotation or cycle is the long-term average number of years required under the prevailing fire regime to burn over an area equivalent to the total area under consideration. As Van Wagner notes, this definition allows for the likelihood that within one fire cycle some stands may burn more than once and others not at all.

The notations in table 1 for fire regimes that involve combinations of short interval surface fires that do not kill most trees, and longer interval severe fires that do result in overstory kill, need explanation. The "fire regime types" are those defined earlier in this paper, and where combinations occur, the overstory regime number is shown above the slash, and the understory regime beneath it. For example, 5/2 means that the overstory regime is one of "long return interval crown fires and severe surface fires in combination," while the surface fire regime is one of "frequent light surface fires." The same practice is followed for the fire cycle notations. There, 150/25 means that the cycle for total stand replacement due to overstory kill is 150 years, while the cycle for light surface fires that kill fewer trees is 25 years.

With this understanding, now let me summarize the continental pattern of fire regimes in northern ecosystems during "presettlement times"--recognizing that for some regions these fire regimes still prevail:

- (1) In arctic and alpine tundra, fires of large size were rare and fire cycles were very long--perhaps so long that fire should be regarded as a disturbance to which the species have not necessarily evolved adaptations.
- (2) At treeline, both in the arctic and in Rocky Mountain alpine situations, fires did occur, but the average fire cycle for such situations was apparently very long (500 years?) and some local sites are virtually fireproof. When the forest does burn at treeline a very long period of forest recovery should be expected because tree reproduction and growth are very slow and uncertain and the tundra/forest balance is delicate. Semipermanent changes in treeline can be expected after severe fires.
- (3) In the main boreal forest regions of Canada and interior Alaska the dominant fire regime was one of high intensity short to long return interval crown fires or severe surface fires, of large to very large size (more than 1,000 acres [400 ha], and often more than 10,000 acres [4 000 ha]). Fire cycles were apparently shorter in the drier regions of northwestern Canada and interior Alaska, where they may have averaged 50 to 100 years, than in eastern Canada where the climate is distinctly wetter. Fire cycles were probably longer near treeline in the open subarctic spruce-lichen woodlands than in the closed boreal forests farther south. In some jack pine forests in western Canada and perhaps also in some lodgepole pine forests, creeping surface fires of low intensity occurred at intervals of 25 years or so, without killing whole stands. Such forests are open in character, and have a multiaged stand structure as a result of this history. Throughout the boreal forest, fires occurred in random patterns due primarily to lightning-caused ignitions and there was much reburning of younger stands. Fire boundaries tend to be very sharp and easily identified on aerial photographs from the air, or on the ground. Unburned older forests often occur as long, narrow "stringers" that somehow are missed by many fires. The longest fire cycles were probably in white spruce forests on the floodplains of major rivers where cycles may have been as long as 200 to 300 years. Perhaps some floodplain forests never burned.

- (4) The subalpine forests of the northern Rocky Mountains had complex fire regimes that varied with elevation and vegetation types. In lodgepole pine forests near the lower ecotone with Douglas-fir savanna the most common regime was one of light to moderate intensity surface fires of medium size (101 to 1000 acres, 41 to 400 ha), with fire cycles averaging near 25 years, that killed only portions of stands--producing a multiaged structure. In some of these stands there may also have been longer cycles of severe crown fires or surface fires that did kill most trees--perhaps on cycles averaging near 150 years. In the middle subalpine zone, mixed forests of lodgepole pine, Engelmann spruce, and subalpine fir generally experienced high intensity crown fires, or severe surface fires of medium to large size that killed and regenerated most of the stand on cycles of 50 to 150 years--cycle length depending on physiographic and climatic factors. In other areas, such as the Bitterroot Mountains of western Montana, lodgepole pine-spruce-fir forests in mid-subalpine situations often had regimes of surface fires on cycles of about 25 years, with only partial stand kill being usual. In the upper subalpine, in mixed Engelmann spruce, subalpine fir, lodgepole pine, limber pine (or whitebark pine) types, the most common regime was one of high intensity crown fires or severe surface fires killing most of the stand, but on long cycles varying from 100 to 300 years. Most such fires tended to burn out before reaching treeline, but some did reach treeline and continued on up into tundra.
- (5) In the Aspen Parkland the characteristic fire regime was one of the short return interval prairie fires sweeping into the parkland from the open prairies on cycles of perhaps 10 years, penetrating deeply into the aspen savannas, and killing back invading trees, thus maintaining the savanna.
- (6) In the Great Lakes-St. Lawrence and Acadian forests there were several distinct fire regimes, depending upon vegetation types and the subregional climatic and physiographic setting. In the north, enclaves of boreal forest had fire cycles very similar to those in the full boreal forest. Red pine and white pine forests on xeric landforms in the Northwest had combinations of moderate intensity surface fires that scarred individual trees, but killed few mature trees, at cycles of 20 to 40 years, with more intense killing fires on cycles of 150 to 200 years. Farther east, and on more mesic sites white pine-red pine forests had regimes of severe crown fires or surface fires that killed much of the stand and brought in new age classes, but on much longer cycles--perhaps 200 to 300 years. "Jack pine barrens" probably had regimes of light surface fires with cycles as short as 15 years, and killing fires that eliminated most old trees on cycles of 60 years. The more southerly and mesic northern hardwood-conifer forests had longer fire cycles--perhaps as long as 300 to 400 years, but fire was still apparently essential in maintaining a component of shade intolerant pines, oaks, yellow birch, cherry, and similar species. Northern hardwood forests lacking conifers probably had still longer fire cycles, but the composition of most forests was probably related to past fires.

Present Fire Regimes

The pattern of changes in fire regimes due to fire control and modification of ecosystems is easily summarized for the North. There are basically two situations, with some intergrades: (1) In the unexploited boreal forests of northern Canada and Alaska the presettlement fire regimes still persist, because man has either not attempted fire control, or his efforts have so far had little effect, and man-caused ignitions are not a significant contribution to the total area burned in most regions. (2) In the Rockies, the exploited boreal forests, the Aspen Parkland and the Great Lakes-St. Lawrence-Acadian forests, fire control, logging, land clearing, and the development of roads, railroads, utility corridors, and urban areas have so greatly

lengthened and modified natural fire cycles, that they are no longer relevant except to understand the natural ecosystem and in the management of large nature reserves.

Mathematical Models of Fire Cycles

The applicability of proposed mathematical models of fire cycles to northern ecosystems also deserves discussion. Van Wagner's (1978) use of the negative exponential distribution is the simplest approach yet proposed, and it may be the most helpful in quantifying fire cycles from studies of existing forests. It is really a simple graphic model of the age-class distribution that would result if a forest on uniform sites composed of many even-aged stands, each having uniform flammability regardless of age, were burned with a completely random ignition pattern over a long time period. Such a forest tends to have a distribution of age classes that fits the negative exponential--namely, there are far more young stands than old. Some stands escape fire almost indefinitely, while others are burned several times. In the ideal forest of this type, average stand age equals the fire cycle, and the average interval between fires at any single point on the ground also equals the cycle. Van Wagner has shown that three real-world examples of boreal or near-boreal vegetation fit the model fairly well. The model has the advantage that it can simulate possible cycles of fire and logging in combination for forests that are exploited for timber yet subject to some level of destruction by wildfire (a common real-world problem in the North).

I do not propose to develop alternative models, or get into the mathematical theory behind possible approaches. But Van Wagner's model seems applicable and practical for most boreal forest ecosystems, and for reasons I will note shortly, the Weibull equation proposed by Rowe and others (1975) and Johnson and Rowe (1977) seems less satisfactory. First, after a brief period of low flammability following fire of perhaps 15 years, most boreal conifer forests (i.e., jack pine, lodgepole pine, white or black spruce) seem to be almost equally flammable regardless of age. This is especially true during wind-driven crown fires. Second, most boreal forest stands are clearly even-aged. And third, lightning, the major and natural ignition source for most boreal forest fires, seems to work in a nearly random fashion, so that a negative exponential age class distribution is actually produced if the data one uses come from a large enough area. If this is so; then all one has to do to determine the fire cycle for a large area is to collect a random sample of stand ages and then plot the age distribution and fit a fire cycle to that distribution. This appears feasible for vast areas of the boreal forest where neither man-caused ignitions nor fire control operations have yet seriously altered natural fire cycles.

Apparently, the Weibull equation suggested by Rowe and others (1975), Johnson and Rowe (1977), and Johnson (1979) forces one to accept a theoretical age class distribution that could not persist under a stable fire regime. The problem is that in any stable regime of forest age class renewal there must be a higher percentage of area occupied by the youngest age class than for any subsequent class, and subsequent classes must also show a decrease in percent of total area occupied. If there are increases, then an age class bulge is present, and the distribution cannot persist indefinitely. Apparently the Weibull equation leads to such a situation.

On the other hand, the negative exponential calls for assumptions that are not fulfilled by some vegetation types in the Great Lakes-St. Lawrence forests and other regions. The most serious of these is probably the requirement of uniform flammability with stand age. There is a convincing argument that natural red and white pine forests become more vulnerable to stand kill with advancing age--particularly if there is invasion by fir, spruce, and white-cedar understories as stands mature, and if periodic surface fires that might reduce or eliminate these understories are withheld. This same criticism would apply in using the model for ponderosa pine, Douglas-fir, or giant sequoia. Fires that kill out overstory trees in such forests are hardly random events--they occur when fuels build up to the point where stand kill is possible.

In fact, both the negative exponential model and Weibull equation hardly fit forests where the natural fire regime was a combination of light surface fires at relatively short intervals and more severe fires at longer intervals--the latter killing out and regenerating portions of such stands. These regimes produce stand age structures too variable and complex to model with a single equation.

THE ROLE OF FIRE IN REGULATING VEGETATION STRUCTURE

In presettlement times the vegetation of many northern ecosystems was structured by fire in three ways: (1) in species composition, (2) in the vertical stratification or arrangement of life forms, and (3) in the horizontal arrangement of plant communities--i.e., the spatial patterns of the vegetation mosaic. Let us look briefly at each.

Effects on Species Composition

In virtually all northern ecosystems the prevailing fire regimes of presettlement times produced a mix of species in each habitat that was adapted to the frequency and intensity of fire likely to occur there.

For example, in most boreal forests, in the middle subalpine zone, and in the enclaves of boreal vegetation within the Great Lakes forests, the most abundant dominants in the conifer forests were genetically adapted to large, short cycle, intense crown fires. The three species that clearly qualify here are jack pine, lodgepole pine, and black spruce. All have persistent, closed or semiclosed cones, and early sexual maturity that guarantee seed dispersal, even if virtually every living tree is killed over wide areas at intervals as short as 20 years (Fowells 1965). Average boreal forest fire cycles are much longer than this--but the random nature of lightning-caused fires means that some stands will be reburned at much shorter intervals. Finds of jack pine and black spruce wood and cones associated with charcoal in old glacial deposits, plus other paleoecological evidence, support the theory that these species evolved under fire regimes similar to the present, hundreds of thousands or even millions of years ago (Rosendahl 1948, Heinzelman and Roe 1963, Mirov 1967, Yeatman 1967).

Quaking aspen, bigtooth aspen, and paper birch are also adapted to short cycle high intensity fires of large size because of their ability to sucker from the roots (aspen) or resprout from the root collar (birch). The aspen and birch also mature sexually quite early, and have very light seeds easily carried long distances by the wind (Fowells 1965). Even white spruce and tamarack, which lack the persistent closed-cone habit, still have very light seeds that enable them to recolonize burns far from living seed trees (Zasada 1971). White spruce must have survivors (unless the fire occurs in the fall of a seed year), but in most fires there are skipped areas, such as floodplains, ravines, islands, lakeshores, or the "stringers" of white spruce that somehow often are left by fast-moving crown fires. Ground layer species are also well adapted to these intense fires--most shrubs resprout from the root collar, some herbs also resprout, and many shrubs and herbs have seeds carried long distances by birds or wind. Mosses and lichens have a complex natural recovery sequence that seems to guarantee their reestablishment also.

The opposite type of fire regime also occurred in certain areas--short cycle, low intensity surface fires, with high intensity surface fires or crown fires that killed overstory trees coming only at very long intervals. As we have seen, such regimes characterized some of the most xeric boreal forest sites, the lowest zones of the subalpine forests, drier red pine-white pine sites of the Great Lakes forest, and the xeric pine barrens of the Lake States. Such fire cycles produced the open red and white pine groves characteristic of much of the original pine forest of the Lake States and southwestern Ontario. Their thick insulating bark and long clear trunks

make red and white pine well adapted to such fire regimes. They also were much better adapted to such a regime than to short cycle crown fires because they do not bear many cones until 50 or 60 years of age, and good seed years are infrequent (Fowells 1965). Mineral soil or thin ash seedbeds are helpful for seedling establishment, and at least sizable stand openings are necessary because of their light requirements. But their longevity (200 to 400 years) permitted red and white pine to take advantage of the occasional large stand openings produced by more severe fires at longer intervals--and the relief from frequent surface fires that may have followed such episodes (Horton and Bedell 1960, Van Wagner 1971). Such fire regimes may also have been essential in keeping down competition from several shrubs, especially beaked hazel (Corylus cornuta) (Buckman 1964).

Oddly enough, jack pine and lodgepole pine also seem adapted to short cycle light surface fires in certain regions, even though they are also the classic examples of species adapted to close interval crown fires. Where they existed under short interval surface fires these fires were clearly of quite low intensity, because the cambium is easily killed by hot fires in both species. On the xeric sites where such regimes prevailed, the stands were evidently open enough, and the trees widely enough spaced so that not much fuel buildup occurred in the 10- to 40-year intervals between fires. In at least several of the regions where such regimes occurred, many trees are of the open-cone variety--a genetic adaptation to such fires (Fowells 1965, Loope and Gruell 1973).

Quaking aspen and bur oak were the most characteristic trees of the Aspen Parkland because of their ability to cope with the short return interval prairie fires that kept the region a savanna--aspen because of its ability to sucker back even if burned at 10- or 15-year intervals, and bur oak because its thick bark makes it extremely resistant to surface fires. The prairie grasses, herbs, and shrubs themselves, of course, are well known for their ability to withstand repeated short cycle fires (Vogl 1974).

Where fire cycles were long, or fire was perhaps even an uncertain or rare event, the dominant tree species again reflected that situation. In the boreal forest, floodplains were occupied by nearly pure white spruce--a species not requiring fire for its perpetuation, and shade tolerant enough so that new generations could persist even if flooding or fire rarely intervened. In the Great Lakes-St. Lawrence and Acadian regions the forests were quite diverse in environments not subject to much fire. If fire did occur, but on cycles to 150 to 300 years, white pine was often dominant in the east, along with mixtures of yellow birch, oaks, and sometimes hemlock, red spruce, sugar maple, beech, and other hardwoods. In the northern Lake States, areas with long fire cycles were likely to support mixtures of white pine, white spruce, balsam fir, northern white-cedar, red maple, and in Michigan and Wisconsin also hemlock, sugar maple, and other hardwoods. Such forests reflected a composition transitional between the boreal and deciduous forest regions, but with species selected for their ability to persist for long periods without fire.

In the subalpine region of the Rockies, the long fire cycles of the upper elevations near treeline permitted such fire-sensitive species as the Engelmann spruce, subalpine fir, and whitebark and limber pines to dominate. These species are all moderately tolerant of shade, and capable of persisting for very long periods without major disturbances. They lack specific adaptations to repeated fires. In New England, the stunted balsam fir forests of the essentially fire-free subalpine zone regenerated in waves of mortality due to wind, needle desiccation, icestorms, and other factors (Sprugel 1976).

One final but critical aspect of the effect of fire on species composition must be emphasized. It is the importance of season of burn with respect to humus consumption in northern forests. Late summer and early fall fires in dry years may burn off

almost the entire organic layer, while spring and early summer fires usually do not. The relationships between drought conditions and humus consumption have been fairly well quantified (Chrosciewicz 1968, Van Wagner 1972). Most lightning-caused fires burn in mid- to late summer, while man-caused fires in most regions show spring and fall peaks. Humus consumption is critical in the establishment of good seedbeds for the pines, black and white spruce, aspen, and birch. The intense ground fires of late summer can therefore be critical in determining which trees succeed. At the same time, if humus consumption is total, and certain shrubs and herbs that normally resprout are rooted totally in the humus layer, those species may be slow in reestablishing themselves on intense summer burns (Ohmann and others 1973).

EFFECTS ON STRATIFICATION OF LIFE FORMS

Short cycle crown fire regimes in the boreal forest often create a simple two-layered vegetation, with only an overstory of fire-dependent conifers (jack pine, lodgepole pine, or black spruce), and a ground layer of mosses, herbs, lichens, and low shrubs. If the period between burns becomes longer, then a multilayered tree canopy may result, with the development of balsam fir, subalpine fir, or northern white-cedar understories. In such cases white spruce and birch are also likely overstory dominants. A tall shrub layer of alder (Alnus crispa) or other species may be present. Where black spruce grows in mixture with jack pine or lodgepole pine it often occupies a subdominant or even understory position in the canopy, but age studies show that the spruce becomes established soon after the fire, just as do the pines. Black spruce simply grows slower.

In red pine-white pine forests in northeastern Minnesota, northwestern Ontario, and a few localities in northern Michigan and Wisconsin, short return interval low intensity surface fires prevented the development of understories of balsam fir, white spruce, northern white-cedar, red maple, and other shade tolerant invaders (Methven and Murray 1974). Balsam, spruce, and cedar understories create ladder fuels that can carry fire into the crowns of red and white pine--and it was clearly necessary that this not occur extensively if the latter were to reproduce. Such fires also prevented the expansion of tall shrub layers of hazel, alder (Alnus crispa and A. rugosa), mountain maple (Acer spicatum), and other species (Buckman 1964). Fire exclusion is now encouraging the development of both types of understories.

Farther south and east, periodic surface fires in white pine may have kept back understories of shade tolerant hardwoods and tall shrubs, although it is not clear that this was common. Where it happened, it may have had the effect of keeping the forest flammable so that eventually a fire severe enough to bring in regeneration could occur.

The so-called "Aspen-Birch-Conifer forests" of Marschner (1930) were aspen and birch stands with understories (or codominants) of balsam fir, white spruce, northern white-cedar and white pine. Here the conifer understories helped guarantee that any large fire that swept the region would also kill and regenerate the aspen and birch. Balsam, white and black spruce, and northern white-cedar fulfill the same function in many sections of the boreal forest. Fire control is increasing the area of aspen-birch forests of this type throughout the northern Great Lakes-St. Lawrence region, with the effect that such forests are again becoming flammable.

Effects on Spatial Patterns of the Vegetation Mosaic

Fire intensity and frequency are among the principal factors that determine whether the vegetation units of a forest region will consist of fine-scale mosaics of small groups of trees of varying ages, or alternatively, of large even-aged stands. A regime of short cycle low intensity surface fires that only kill occasional groups of older trees will produce a fine-scale mosaic of many-aged groups. Such vegetation

patterns were characteristic of the presettlement forests in the following regions:

- (1) Some lower elevation lodgepole pine forests in the subalpine zone of the Rock Mountains, from at least north-central Alberta south to Wyoming (Loope and Gruell 1973, Houston 1973, Habeck and Mutch 1973, Gabriel 1976, Arno 1976, Tande 1977).
- (2) Some jack pine forests of sand plains and other xeric land forms in the western boreal forest of Canada (Rowe and others 1974).
- (3) Jack pine forests on the xeric sand plains of Wisconsin, Michigan, and local areas in Minnesota (the "pine barrens").
- (4) Red pine-white pine stands on certain frequently burned sites in Minnesota and elsewhere in the western Great Lakes forests (Frissell 1973, Heinzelman 1973).

Conversely, a regime of high intensity crown fires or severe surface fires will produce even-aged stands in forests adapted to such regimes. As we have seen, many boreal forest vegetation types and some of the middle elevation subalpine types are well adapted to such regimes. It is important to recognize that the typical patch size and shape characteristic of such vegetation types depends on the size and shape of the ecologically significant fires that have burned during a full fire cycle, and on the extent of reburning of stands within that cycle. Thus an ecosystem may experience numerous small, low-intensity fires that do not create much change, but only an occasional intense, large scale crown fire. But if such large fires are the principal agents that regenerate the system, then what we see on the landscape is a mosaic of very large vegetation units, sometimes whole forests covering hundreds of thousands of hectares, all of one age class, and often of only two or three dominant tree species. If in our lifetimes we see only small fires or no fires at all on a given landscape, it may be difficult to accept the fact that the forest we know so well is really an aging postfire stand that in the natural course of time would burn again. But this is the way the system has been in the boreal forest and in many Rocky Mountain forests for most of postglacial time.

Typical patch sizes in the boreal forest are probably larger in northwestern Canada and Alaska than farther east. Certainly they average many square kilometers in area in western Canada and Alaska, but even in eastern Canada single age class units typically cover very large areas, and no reliable data are available for comparison. The reports of Methven, Van Wagner and Stocks (1975), and Donnelly and Harrington's (1978) maps make it clear that in the boreal forests of Ontario patch sizes can range up to at least 150 to 270 square miles (390 to 700 square kilometers). Even in the BWCA, typical patch sizes are in the range of 10 to 50 square miles (26 to 130 square kilometers), and some are as large as 160 square miles (414 square kilometers).

In such forests there usually are variation in vegetation types within these large even-aged burns due to such factors as soil changes, depth to bedrock, local relief, slope and aspect, moisture regimes, etc. For example, such factors often control which sites are occupied by jack pine and black spruce as opposed to aspen, birch, fir, and white spruce, with the latter group on the more fertile and mesic sites. But often areas as large as 20 to 100 square miles (50 to 260 square kilometers) are essentially all one age class--resulting from a single burn--regardless of the diversity of vegetation types included. Certainly there are small areas of older age classes, usually around lakes, rivers, sharp breaks in topography, and similar areas that serve as partial firebreaks, but spot fires ahead of the main fire frequently cross such barriers, and the skipped areas are left as small islands of older age classes within a sea of new forest.

The recent history of northern ecosystems is a mixture of continuing presettlement fire regimes in certain areas, and of vastly changed fire regimes in others. In much of northern Canada and Alaska fire still plays out its ancient role, and the kaleidoscope of change in the vegetation mosaic still turns--with new forest age classes being generated, largely by lightning-caused fires, at essentially the same rates that have been documented for the recent past. But in the southern boreal forest, the Great Lakes-St. Lawrence and Acadian regions, and much of the Rocky Mountain subalpine region, logging and man-caused ignitions, and more recently fire suppression, have vastly changed the frequency and intensity of fires--and therefore also their effect on spatial patterns of the vegetation mosaic.

In the Great Lakes-St. Lawrence region the effect on spatial patterns has been the greatest. Logging of the pineries, followed by repeated large-scale slash fires and endless small "settler fires," reduced the original complicated patterns of white pine-red pine forests to monotonous and nearly even-aged forests of virtually pure aspen and paper birch. Probably 10 million acres (4 million hectares) of this type of forest were generated on former pine land in the Lake States and southwestern Ontario in the period 1860 to 1920. Reburning and subsequent pulpwood cutting of some of the older and better quality aspen stands has further narrowed the age range in these forests. Thus today there are vast areas of aspen-birch forests on former pine land having average stand ages of 40 to 80 years (Zasada and Heinselman 1954, Stone 1966, Brinkman and Roe 1975). Fire suppression and low rates of commercial harvest on many areas are now permitting succession to replace some of these stands with balsam fir and spruce in the north and hardwoods in the south, but this age class hiatus in the Great Lakes forests will persist to a degree for many years to come (Heinselman 1954).

Fire suppression is also now causing major changes in the spatial patterns of age classes, and in some cases also in vegetation types, in unexploited and lightly exploited forests in the subalpine region of the Rockies, and in a few large nature reserves in the Great Lakes-St. Lawrence forests (the BWCA and Quetico Park in Minnesota and Ontario, the Porcupine Mountains State Park and Isle Royale National Park in Michigan, Adirondack State Park in New York, Baxter Park in Maine). Here the effect of fire control has been to allow existing even-aged postfire forests to mature, while replenishment of younger age classes by fire is eliminated or greatly reduced. This is now occurring on a vast scale in the American and southern Canadian Rockies because very large areas are in National Parks and Wilderness Areas where logging is excluded, and many other areas are not economical to log.

On many of the deforested or naturally open sand plains of the Lake States and on abandoned farms throughout the Great Lakes-St. Lawrence region, red pine and a few other conifers have been widely planted since about 1934. Many plantings have been pure red pine, and spacings have been close (Rudolf 1950). Such plantings have created large expanses of highly flammable single age class, single species stands with tightly interlocking crowns, sometimes in areas where the presettlement forest was an open pine savanna.

Most commercial pulpwood harvesting of jack pine and black spruce has been by clearcutting. Such a practice simulates one of the natural effects of fire by opening up the cut areas to full sunlight. If followed by prescribed burning of slash, the natural seedbed preparation effects of fire would also be achieved. Research has shown that clearcutting, followed by slash burning and seeding or planting of black spruce and jack pine is effective (Ahlgren 1970; Johnston 1971a, b, 1973; Benzie 1973). With black spruce, strip and patch clearcutting can also be effective. Unfortunately, the known techniques for regenerating these species have often not been applied, and many recent cutover areas now support a mixture of species and age classes that has greatly altered the original even-aged spatial patterns.

As noted earlier, fires at treeline adjacent to either true arctic or alpine tundra can lead to long periods of forest recovery, or even semipermanent replacement of forest with tundra vegetation. Black and Bliss (1978) report that some burns near Inuvik, N.W.T., in open black spruce-lichen woodland at the forest-tundra ecotone have led to semipermanent shrub-dominated vegetation within the last 100 years. There is substantial evidence that fires have been involved in quite widespread southward shifts of the subarctic treeline in the N.W.T. in the past 5,000 years, but climatic change, not fire, seems to be the underlying cause (Larsen 1965, 1971; Ritchie and Hare 1971; Black and Bliss 1978).

THE INFLUENCE OF VEGETATION STRUCTURE ON FIRE FREQUENCY AND INTENSITY

This section, when contrasted with the previous one, poses the classic "chicken and the egg dilemma." Most of what needs to be said here has already been said in the reverse context of the last section. A few principles and comments on the present situation are worth setting down.

First, a general principle in the north is that conifer forests are more flammable than deciduous forests, and extensive conifer forests in most of northern North America have crown fire regimes. Once crown fires have occurred in vegetation capable of reproducing quickly under such fire regimes, extensive areas of even-aged conifer stands are generated. Where lightning is available as an ignition source, and fire suppression is not effective, such forests will perpetuate a regime of periodic intense crown fires at frequencies (cycles) long enough to permit regrowth and effective sexual reproduction of the flammable conifers involved. If it were otherwise, the even-aged boreal conifer forests would not exist, nor would many of the lodgepole pine forests of the subalpine region, and some of the near-boreal vegetation of the Great Lakes-St. Lawrence forests.

Another principle is that the slash left after clearcutting of northern conifers will create a fuel type that if burned greatly changes the subsequent forest vegetation unless man intervenes or a standing forest is left within seeding range. Fires in logging debris simply do not produce a vegetation comparable to that resulting from crown fires or severe surface fires in standing timber. When slash is burned, the cones and seeds of the potential parent trees are imbedded in the fuel matrix, and the heat of the slash fire will normally kill most or all of the seeds. Slash fires may very well create desirable seedbeds, but direct seeding or planting are required to regenerate the forest unless an uncut forest exists within seeding range (Beaufait 1960, 1962; Ahlgren 1970; Johnston 1971). Failure to burn the slash can result in uncontrollable wildfires (Sando and Haines 1972). If such fires do not occur, the regeneration is still unlikely to duplicate the original forest without seeding, planting, or other direct action by man.

Today, in the Great Lakes-St. Lawrence and Acadian forests the forest landscape is so broken up by agricultural lands, roads, railroads, utility corridors, and urban areas that the fuels complex lacks the continuity it possessed in presettlement times. Many of these human influences create firebreaks that are effective in stopping low intensity fires. Some of the larger agricultural and urban areas would also be effective in checking even fast-moving mass fires.

But the periodic severe droughts that are sure to come again can generate climatic situations favorable to large-scale fires. And once fires in northern conifer forests gain headway under extreme burning conditions, their spread is difficult to check until weather conditions change, fuels are exhausted, or truly effective firebreaks are reached. Roads and other rights-of-way are seldom wide enough to check such fires. Two Badoura, Minn., fires that burned in jack pine, red pine plantations,

and meadow-grass in virtually the same areas in 1959 and 1976 demonstrate how difficult it can be to control such fires even with modern equipment in a well roaded area. The 1976 Huntersville-Badoura fire burned 24,000 acres (10 000 hectares) in just 18 hours, and made a maximum run of 9 miles (14 km) in 5-1/2 hours, 4 miles (6 km) of which occurred within 1 hour (Wickman 1976). This fire was fought with aircraft tankers, helicopters, retardants, bulldozers, pumps, and other modern gear. But the fire was not controlled until the winds died and a light rain fell.

The Great Lakes-St. Lawrence region has a history of tragic mass fires in developed areas, and such fires may still be possible. Modern road networks and firefighting equipment have greatly reduced the risk. But the Huntersville-Badoura fire should be a warning. The extensive young pine plantations of many developed regions have added a new ingredient, and the old ingredient of extreme fire weather will surely appear again (see Arnold 1968). Conditions for the start and spread of crown fires are now fairly well known for this region (Van Wagner 1977a,b; Stocks 1977).

FIRE AND SUCCESSION IN NORTHERN FORESTS

True succession--in the sense of one vegetation complex replacing another on a given site in the absence of disturbance--rarely occurred in presettlement times in the boreal forest, in most of the subalpine of the Rocky Mountains, and even in much of the Great Lakes-St. Lawrence and Acadian forest. Certainly two-layered forest stands are common in the boreal forest, in many subalpine forests, and in some near-boreal vegetation types of the northern Great Lakes-St. Lawrence forests. Frequent overstory/understory combinations are: (1) jack pine over black spruce or balsam fir; (2) quaking aspen and paper birch over balsam fir, white spruce, northern white-cedar, or black spruce; and (3) lodgepole pine over Engelmann spruce, subalpine fir, white spruce, or black spruce. Often the overstory trees are considerably taller and larger in diameter than the understory species. At first glance these are obvious cases of succession.

But careful investigation of the age structure of overstory and understory components will usually show that these two-storied stands are simply examples of differential growth rates and suppression of slower growing species. Jack pine, lodgepole pine, aspen, and birch have more rapid juvenile growth rates than do the spruces, firs, and northern white-cedar. In my studies in the BWCA (Heinselman 1973) I found that in jack pine/black spruce stands nearly all of the black spruce had seeded in after the fire, just as the jack pine had, but the black spruce nevertheless often formed an understory layer. Methven, Van Wagner, and Stocks (1975) found similar stand-age structures in the western Ontario boreal forest.

Fire exclusion might eventually "force" succession to the more shade tolerant understory species in these cases. Yet even in the BWCA, where fire suppression has been effective almost 70 years, this still has not happened on a significant scale. What one sees is just the gradual maturation of the competing species--and all are capable of living at least 200 years. The absence of fire in such forests is unnatural, and the final end product of fire exclusion is still unclear. As Methven, Van Wagner, and Stocks (1975) state the hypotheses:

- (1) Fire is a normal and necessary component of the boreal forest. The exclusion of fire would be abnormal.
- (2a) Fire in the boreal forest always results in the reestablishment of forest.
- (2b) Whether the same species predominates after fire as before depends partly on the fire frequency and partly on the proximity of other seed sources.

- (3) Seeding in is completed quickly, and all individual young trees capable of taking part in the stand development are present from the start. There is no succession in the normal sense of the term, only a cycling of the forest by fire.

There is a substantial literature on succession in the boreal forest (Damman 1964, LaRoi 1967, Dix and Swan 1971, Rowe and Scotter 1973, Viereck 1973, Grigal and Ohmann 1975, Black and Bliss 1978), but most recent papers recognize the crucial role of fire in these ecosystems. Where man is now breaking the natural boreal forest fire cycle through fire suppression or logging, profound changes in the ecosystem are occurring, and some of these changes may artificially force new combinations of species through processes that were not the rule in nature. Whether such changes can be properly termed "succession" is doubtful. For example, in the southeastern boreal forest fire exclusion causes maturation of balsam fir on a scale that leads to explosion of spruce budworm populations and death of the balsam (Batzler 1969). A comparable discussion involving many of the same tree species is occurring for the subalpine region of the Northern Rocky Mountains (see Habeck and Mutch 1973, Loope and Gruell 1973).

In the Great Lakes-St. Lawrence white pine and red pine forests, certain stand structures have also been cited as evidence of succession. Examples are: red and white pine with understories of white spruce, balsam fir, paper birch, black spruce, northern white-cedar, and red maple in northern localities; or white pine with understories of hemlock, sugar maple, yellow birch, beech, red oak, and other hardwoods in Michigan, Wisconsin, southern Ontario, New Hampshire, Maine, and other eastern localities (Cooper 1913, Grant 1934, Graham 1941). But the pine overstories in such stands are capable of persisting for at least 300 to 400 years without fire, and it is unlikely that the other stand elements would simply "succeed" the pines upon their death.

In the BWCA I documented one such stand where the white pine overstory has persisted for about 360 years without fire, yet succession had still not replaced them, and some of the white spruce and balsam fir trees in the "understory" were dying from factors related to their age (a spruce budworm outbreak) just as were many of the pines (Heinselman 1973). Without fire, which would have normally terminated such stand decadence in presettlement times, the ultimate demise of this forest may come through a major windfall which uproots and breaks off not only the pines, but also many of the "successional" understory trees. This could well perturb the system sufficiently to regenerate some of the light-demanding species that normally repopulate burns--perhaps even including white pine. The augmented fuels would certainly invite fire.

A similar situation in New Hampshire was documented by Henry and Swan (1974). In their study area an old white pine forest that originated after a fire in about 1665 persisted for 273 years, but was finally destroyed by a series of 4 windstorms--culminating in the 1938 hurricane. At the time of its demise, 55 percent of the main canopy of the old stand still consisted of postfire stems that had germinated between 1665 and 1702. The disturbances that finally terminated this stand's existence were so severe that they initiated a whole new forest, albeit one somewhat different in composition from the one destroyed by wind. The authors conclude that "...autogenic succession--a directional change in composition--could not be clearly defined during the 273 years between severe disturbances, although an increase in the proportion of hemlock was indicated."

The cessation of periodic low-intensity surface fires in many old red and white pine stands in the Great Lakes-St. Lawrence forests due to fire suppression has created a new fuels situation, even if the induced vegetation changes cannot really be accepted as "succession." For example, in the BWCA and Itasca State Park, Minn., many pine stands that bear two or more fire scars from earlier fires now have moderate to dense

understories of balsam fir, white spruce, black spruce, and sometimes northern white-cedar. These flammable conifers, which retain their branches nearly to the ground, are now growing to heights which bring their crowns into contact with the pine canopy, creating fuel "ladders" that can carry lethal crown fires into the overstory. Such understories certainly also developed during the presuppression period, but surface fires of the kinds recorded by fire scars would have held back or eliminated much of this type of understory invasion. If fire suppression is continued, many such stands will develop understory fuel layers capable of generating such intense fires that restoration of the presettlement fuels situation may be difficult without prescribed burning, or even costly understory control through cutting and burning. True succession to a new vegetation type may eventually occur in some of these cases, and the pines will be lost to the ecosystem. But what we are seeing now is just a man-induced aging of both understory and overstory species. This is primarily a concern in National Parks, Wilderness Areas, Research Natural Areas, and State Parks where programs have excluded fire and where the options of using logging, mechanical site preparation, and replanting to pines are unacceptable.

In the subarctic wintering grounds of the barren-ground caribou in northwestern Canada and interior Alaska an opposite concern has been expressed. Here the debate has been over whether an increase in man-caused fires has accelerated the rate of destruction of the open, "climax" spruce-lichen woodlands where many of the caribou herds overwinter. In these open subarctic woodlands there is really no succession in the tree layer. Black spruce, the principal tree, simply reproduces after fire, and eventually recovers its former abundance--creating a partial tree cover of short, stunted open-grown individuals (Black and Bliss 1978). Some 50 to 100 years are required for new tree cover to become significant--the time depending on local conditions. In the absence of fire, black spruce maintains itself by "layering"--a form of asexual reproduction (Black and Bliss 1978).

Following fire there is a progressive change in ground cover species and in the development of tree lichens on the branches of the spruce. Recovery of foliose ground lichens (Cladonia mitis, C. alpestris, C. rangiferina, and Stereocaulon spp.) and tree lichens (Usnea spp., Alectoria spp.) requires 50 years or more (Rowe and Scotter 1973; Scotter 1964, 1970). There is also a clear progression of other lichens and of moss species with time since fire (Maikawa and Kershaw 1978). In some cases in the Lower Mackenzie Valley a prolonged dominance of the shrubs Vaccinium uliginosum, Salix glauca, S. pulchra, and Betula glandulosa may postpone the development of full lichen ground cover to beyond 100 years (Black and Bliss 1978).

Scotter (1964) and others have held that lichens are critical to caribou survival, and that man-caused fires or perhaps changes in the lightning fire regime have increased the rate of burning of these spruce-lichen woodlands to a point where caribou winter ranges are seriously reduced. Bergerud (1974) discounts the importance of lichens, and points out that caribou also utilize sedges (Carex spp.) and many shrubs and herbs that occur on recently burned land. Kelsall, Telfer, and Wright (1977) have reviewed much of the literature on this controversy, and conclude that more should be learned about the relative importance and dietary value of the plants eaten by caribou on various ranges. On the question of changes in fire frequency and intensity on winter ranges, a consensus is developing that most of the area burned is due to lightning-caused fires, and there is no clear evidence of recent increases in burning over most of the regions concerned (Rowe and others 1974; Rowe and others 1975; Johnson and Rowe 1975, 1977; Kelsall, Telfer, and Wright 1977). There may, however, be some long-term fire-related changes underway in forest vs. tundra vegetation near the subarctic treeline due to climatic shifts (Larsen 1965, 1971; Ritchie and Hare 1971).

Let me end this discussion of succession with a final observation. I share with Loucks (1970) the opinion that removing fire from northern ecosystems would be among the greatest upsets in the environmental system that man could impose--possibly among

the most severe stresses since the evolution of the fire-dependent biota involved. I cannot predict the outcome, but a fundamental reordering of the relationships between all plants and animals and their environments would occur. Many species could be lost through extinction.

CONCLUSIONS AND A LOOK AT THE FUTURE

The unexploited sections of the Canadian and Alaskan boreal forest are largely pristine natural environments, little affected by either direct manipulation of their vegetation or by alteration of natural fire regimes. They are among the principal areas remaining on the globe where this is so. Here there are still hundreds of thousands of square kilometers of fire-dependent ecosystems where the fire regimes are certainly natural, because lightning ignitions are responsible for most of the annual burn. But this situation may not last much longer because new roads, airstrips, oil wells, and mines are being developed at a rapid pace throughout the north in both the U.S. and Canada. Both Nations are also considering more active and sophisticated fire management programs. While these programs may and should include decisions to allow natural fire regimes to continue over large areas, the pace of development makes it clear that fire suppression zones will be increasing in numerous previously remote areas.

This situation presents a remarkable opportunity and challenge to the scientific community. For here is a vast display of natural fire-dependent ecosystems, suddenly becoming accessible enough so that research on a considerable scale is feasible, where we do not have to argue about what the "natural," or "presettlement," or "presuppression" fire regimes were. They all exist now. We can study this system in all its complexities, (with a bit of caution near developed areas) with the assurance that fire is a natural functioning environmental factor, driving the system as it always has--before our very eyes. The region is vast enough so that most of the problems of scale--limitations imposed by size of the study area--that plague us so often in National Parks, Wilderness Areas, and Research Natural Areas are not operative. We must not miss this opportunity. There may never be another one.

One simple effort that could be made at once is a survey of the age-class structure of the forest mosaic in representative sections of the Canadian and Alaskan boreal forest. If Van Wagner's (1978) reasoning is sound, then more age class-fire scar studies of the kind conducted by Rowe and his coworkers could quickly document the range of fire cycles in various environments across the continent (Rowe and others 1974, 1975; Johnson and Rowe 1977). Stand origin mapping of the kind Tande (1976) and I (Heinselman 1973) have done may not be necessary to document cycles, although this kind of mapping can be easily done, and should be undertaken at representative sites. It would provide a more direct test of Van Wagner's ideas on fire cycles than did my data, where fire suppression had already changed the fire regime for 60 years, and where logging poses the question of differential loss of the fire record.

In the subalpine forests of the Northern Rocky Mountains, the natural fire regimes of many areas have now been significantly altered by fire suppression, logging, or both. But in these slow-growing high elevation forests the changes in age-class patterns are slow, and the fire scar record lasts a long time. We are beginning to get a picture of the presettlement fire regimes of the region through the work of Arno (1976), Gabriel (1976), Houston (1973), Loope and Gruell (1973), Mutch and Habeck (1973), Tande (1977), and others. But many questions remain, and the forest age class patterns created by centuries of fire history are still on the landscape waiting to be read in large areas untouched by logging. Again, properly designed surveys of the age structure of such forests could help us better understand the variations in fire regimes. A major unresolved question that could be answered by such surveys is the relationship of vegetation types, slopes, aspects, and elevation zones to the prevalence of large-scale crown fires or tree-killing surface fires versus creeping low-intensity

surface fires. Both kinds of fire regimes definitely occurred within these ecosystems, and it will be important for practical fire management programs as well as for ecological theory that we understand the circumstances that produced each kind of regime. Additional stand-origin mapping is needed. Tande (1977) has shown that such mapping is practical and useful in this region. When more such work has been completed, it will be possible to definitively answer additional questions about fire regimes. Tests of Van Wagner's fire regime model for presuppression fire regimes would become possible for additional areas, because once stand origin maps are available, all one need do is subtract the years since suppression began and apply the model to the remaining record.

For the arctic and alpine tundra regions more studies are needed to determine the effects of lightning-caused fires at the forest/tundra ecotone. Fire exclusion may now be causing forest advances into tundra in the Rockies, while at treeline in the subarctic fires may be interacting with climatic change to cause semipermanent changes in treeline. The literature raises many questions, but the answers are not yet clear.

In the Great Lakes-St. Lawrence and Acadian forests the presettlement fire patterns are almost totally obliterated by the cultural actions of man, including particularly logging, slash burning, land clearing for agriculture, fire suppression in the last 60 years, and tree planting in the last 50 years. Man now totally dominates most of the ecosystem, and there are many fire management options that make sense for various situations. These, however, are beyond the scope of this paper. There is still a chance to document the presettlement, or at least presuppression, fire regimes of a few areas with good fire scar chronologies because red pine keeps scars very well, and attains ages up to nearly 400 years in some environments. This work should be done quickly, because there will never be another chance to look at the continent-wide pattern of forest fires prior to man's dominance of the system. (For this purpose white pine is not a very useful species. It often decays quickly after fire injury.)

Another general question that needs work is the relationship of flammability of various northern conifer vegetation types to stand age and to the presence or absence of various kinds of understory strata. There is some indication that flammability does increase significantly with age, and that the potential for overstory kill increases with age and the development of fir and spruce understories in several pine types. But the literature is contradictory, and fire specialists do not agree on all aspects of the question. The applicability of Van Wagner's (1978) fire cycle model to various ecosystems depends in part on answers to these questions.

We need to understand better the linkage between the occurrence of ecologically significant fires in presettlement times and the occurrence of various geographic drought patterns. There are indications that much of the forest burning that produced new forest age classes, or changes in stand structure where fires were not totally lethal, occurred in widely time-spaced major drought years. Some of these drought years were synchronous over large sections of northwestern, north-central, or northeastern North America. Some apparently were even synchronous over much of the continent east of the Cordilleran Mountain system. The evidence for this comes from the widespread occurrence of forest fires in certain years, as determined from fire scar dendrochronologies, and from the existing climatological data for recent fire years. Some of the agreements in fire years that have come to my attention are shown in table 2.

We need to understand the atmospheric phenomena that lead to potential fire years of this magnitude. Such knowledge would help greatly in recognizing the fire potential of future droughts as they develop, and it would also help elucidate the probable recurrence patterns of major fire years in various regions of the northern continent. Actual prediction of fire years is surely a long way off, but that too is among the potential payoffs of such research.

Table 2.--Major fire years in northern North America occurring in widely separated regions

Fire Year	Interior Alaska Barney, Lutz, Viereck Mackenzie Valley Rowe	Alta., Sask., Man., N.W.T. Scotter, Kelsall Inuvik, N.W.T. Black, Bliss Arctic Tundra Wein	Jasper Natl. Park., Alta. Tande	Bob Marshall, Mont. Gabriel	Northern Idaho, Mont. Wellner	Bitterroot Natl. For., Mont. Arno	Glacier Natl. Park Habeck	Yellowstone Natl. Park Houston	Grand Teton Natl. Park Loope, Gruell	Estes Park, Colo. Clements	Itasca Park, Minn. Frissell	BWCA, Minn. Heinselman	Northern Wis. Haines, Swain, Grange	North West Ont. Stocks, Methven, Van Wagner	Pukaskwa Natl. Park, Ont. Alexander	Northern Michigan Haines, Sando	Algonquin Natl. Park, Ont. Cwyner, Burgess	Quebec Van Wagner, Methven	New Brunswick, Maine Wein, Moore
1976											X							X	
1974			X								X		XX						
1971			XX								X		X					X	
1969	XX	XX	XX																
1961		X			X	XX								XX			X	X	
1957	XX																	X	
1950	XX	X																	
1947	XX		X														X		
1940	XX	X			X														
1936				X								X							
1935	XX					X											X		
1917		XX		X													X		
1914				X													XX		
1911		XX		XX						X									
1910				XX	XX	X					XX	X			XX				
1905		X		X		X			X	X	X								
1898	X	X		X		X													
1894	X	X					X	X	X		X	XX	XX						
1892		X		XX		XX		X		X	XX								
1889		X	X	XX	XX	XX	XX				X	X					XX		
1881		XX		X		X						X				XX	X		
1875				X		X		X		XX	XX						XX		
1871						XX		XX		X	X	XX							
1864		XX		X		X		X	XX	XX	XX	X					XX		
1854				X							XX						XX		
1846			X	X		XX					X						X		
1824				X		XX		X			XX								XX
1803		XX		X		XX		XX			XX	X							
1796			X								X	XX							
1784						XX		XX				X							
1766						X		X	X			X							
1758			X			XX		XX			XX	XX					X		
1755						X			X			XX							
1747						X		X				X							
1727			X					X			XX	XX							
1714			X			X		XX											
1695						XX						XX					X		
1692						X		X											
1681						X						XX							
1667						XX		X											
1627						X		X											
1610						X		X				X							
1595						X		X				X							

XX=Major fire year at indicated site.

X=Significant fire year at indicated site.

There is a need for more attention to historic fire patterns in land use planning in the north--especially in undeveloped regions where options are still open. We know that major drought years will occur again, and that certain vegetation types have a high probability of supporting uncontrollable, fast-moving crown fires. It is folly to build homes, towns, or other costly structures in such vegetation types--particularly on sites where fire suppression would be difficult under probable scenarios. We know enough to define such sites, and fire managers have an obligation to communicate this knowledge to decisionmakers.

I am pleased that this symposium has brought together such a wide representation of talents, disciplines, and geographic regions to look at the role of fire in ecosystems. We need to see fire as a powerful and pervasive environmental factor to which many of the earth's most widespread and significant ecosystems were somehow attuned. Research into the role of fire in ecosystems deserves high priority because the results promise to contribute much to our understanding of ecosystem processes, and to general ecosystem theory. In systems where natural fire was a significant factor, all of the plants and animals in such systems must have evolved strategies to use, endure, or somehow cope with fire, else they could not have survived. Our opportunities to understand natural fire are fading rapidly because of the press of human numbers on our planet. If we are ever to understand how fire shaped the organisms and natural vegetation of the world we must do so soon. And many of the answers may come from the northern conifer forests of North America, where the natural record still lies open--waiting for eager young minds to read it.

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FIRE IN ECOSYSTEM DISTRIBUTION AND STRUCTURE: WESTERN FORESTS AND SCRUBLANDS

Bruce M. Kilgore

Associate Regional Director, Resource Management and Planning,
Western Region, National Park Service, San Francisco, Calif.

ABSTRACT

Fire plays an important role in determining structure of forests and scrublands throughout the West. Distribution and structure of vegetation depends upon topography, climatic regime, and fire regime. Six fire regimes are defined based on fire frequency and intensity, varying from frequent, low-intensity surface fires to very long return interval, stand replacement fires. In certain western forests and scrublands fire suppression for the past 50 to 100 years has led to longer intervals between fires, increases in surface and crown fuels, changes in forest structure, and sequential impacts on fire intensity, postfire age structure, species composition, fuel accumulation, and both horizontal and vertical pattern. Better understanding of fire regimes is basic to our management of western ecosystems.

KEYWORDS: western forests, fire regimes, fire frequency, fire intensity, scrublands.

INTRODUCTION

Fire plays a major role in the function of most of the forests and scrubland ecosystems of the western United States. In many ecosystems, fire controls the age structure and species composition of the vegetation and creates a mosaic of vegetation types on the landscape (Heinselman 1978). Fire acts with different frequencies and intensities, depending upon the vegetation and topography involved, as well as the climatic regimes which determine the coincidence of ignitions with given burning conditions. Thus vegetation composition and structure depend on climate, fire frequency, and intensity, while fire frequency and intensity in turn depend on vegetation structure, topography, and climatic regimes.

Because of almost annual coincidence of ignitions with suitable burning conditions, western forests, such as those found in the Sierra Nevada, have frequent fires. Because such fires are frequent, they are of low intensity. By contrast even though ignitions are equally as frequent in certain Rocky Mountain forests, they do not coincide as frequently with dry fuel conditions. Thus these fires have a longer recurrence interval and are either more intense surface fires that kill all nonresistant species or are crown fires with shorter or longer return intervals.

Forest and scrublands in the West can be grouped into the following four broad formations adapted from Oosting's (1956) climax formations of North America: (1) subalpine forest, (2) montane forest, (3) woodland, and (4) scrubland. These formations--based on climatic regime and topography--range from vegetation found in moist, higher elevation, north exposures to that found in drier, lower elevation, south exposures. These formations occur in altitudinal zones on the principal mountain ranges in the West: the Rocky Mountain, Cascades, Sierra Nevada, and Coast Ranges as well as on Great Basin and Intermountain ranges. Distribution of plant communities or habitat types in the western United States has been covered broadly by Oosting (1956) and in more regional detail by Daubenmire and Daubenmire (1968), Franklin and Dyrness (1973), Munz and Keck (1959), and Pfister and others (1977).

Impact of Fire Frequency on Species Composition

Frequency of fire is critical in selecting those species that will continue as part of the vegetation of a given area. A species cannot survive if fire is introduced too often or too early or deferred too long in its life cycle (Hendrickson 1972). For example, with nonsprouting species, survival in a given area may be threatened by fires which occur before there has been time for a seed pool to accumulate or after the plant's longevity has been exceeded and the store of seed is lost (Gill 1979). The significance of fire frequency in determining the species composition aspect of forest structure through time is illustrated when fire burns often enough to prevent a fire-dependent Douglas-fir (Pseudotsuga menziesii) or lodgepole pine (Pinus contorta) forest from changing to a nonfire-dependent, shade tolerant fir, cedar-hemlock, or spruce-fir forest.

Impact of Fire Frequency/Intensity on Vegetation Mosaic

The horizontal pattern or mosaic of vegetation in a given area is made up of contrasting age classes, successional stages, and vegetation types created by recurring fire over long- or short-term rotation periods (Heinselman 1978). The scale of the vegetative mosaic is influenced by frequency and intensity of fire as well as the topographic base on which fire occurs. In relatively flat or gently rolling country where long-term intense crown fires or stand-replacing surface fires are characteristic, patches of the mosaic may cover thousands of acres. In steep, broken terrain, such as the Sierra Nevada, where low-intensity fires burn frequently, the patches may be less than 0.25 acres (0.1 ha) in size (Bonnicksen 1975). Whatever the size of patches or aggregations involved, the overall mosaic changes little, as long as the frequency and intensity of fire characteristic of that vegetation and topography continues; the individual aggregations are periodically rearranged by fire and succession, like pieces of a kaleidoscope (Bonnicksen and Stone 1978, Heinselman 1978).

Fire Regimes

Fire is important in so many ecosystems that it is becoming less meaningful to refer to fire-dependent vs. fire-independent systems. Instead we need to speak of systems with varying "fire regimes" made up of such factors as fire frequency and intensity (Heinselman 1978, Sando 1978), season (Gill 1973), pattern (Keeley 1979), and depth of burn (Methven 1978). In order to emphasize the wide range of fire characteristics found in the West and to make comparisons between them, I have organized what is known about the impact of fire frequency and intensity on vegetative structure around a modification of the fire regimes described by Heinselman (1978):

- (1) frequent, low-intensity surface fires (1- to 25-year return interval);
- (2) infrequent, low-intensity surface fires (more than 25-year return interval);

- (3) infrequent, high-intensity surface fires (more than 25-year return interval);
- (4) short return interval, stand-replacement fires (25- to 100-year return interval);
- (5) variable regime: frequent, low-intensity surface fires and long return interval, stand-replacement fires (100- to 300-year return intervals); and
- (6) very long return interval, stand replacement fires (more than 300-year return intervals).

Certain major forest types are covered only briefly because little is known at present about the relationship between forest structure and fire frequency and intensity in those types. More thorough treatment has been given here to certain other forest types--particularly the sequoia-mixed conifer forest--because information is available, even though the type covers a more restricted geographic range.

An intense fire can either burn through the tops of crowns of trees, thus killing trees as a "crown fire," or it can simply girdle or heat-kill fire-sensitive trees by intense burning at ground or surface level. In either case, the stand of trees or segment of the forest is partially or totally killed. However, only in the most short-term sense can this be called simply a "stand-destroying" fire. Because at the same time it is killing the existing group of trees, the fire is providing a set of conditions--sometimes involving the seedbed, opening of closed cones, or stimulation of sprouting species--which lead to replacement of the old forest or scrubland by a new vegetation. In this paper, therefore, a high-intensity surface fire or crown fire which kills most of the existing vegetation is also referred to as a "stand-replacement" fire as used by Gabriel (1976), Habeck (1976), Antos (1977), Sneek (1977), Van Wagner (1978), and Arno (1980).

Fire frequencies are difficult to compare in a meaningful way between different studies of various forest types and geographic regions unless similar-sized units are being compared. Kilgore and Taylor (1979) used "frequency" to mean "interval between fires on the same piece of ground...calculated from records found on a single tree or a cluster of trees growing fairly close together." C. E. Van Wagner (personal communication) feels there is only one basic parameter, namely, "the average number of years between fires at a point." He notes, however, that "fire cycle" is the same concept if it is defined as the number of years to burn an area equal to the whole area in question (see also Methvan 1978). This is similar to Heinzelman's (1973) "natural fire rotation," and "fire return interval" (Tande 1977) embodies the same idea. "Fire frequency" or "fire cycle" can be contrasted with "fire incidence" which has been defined as "the interval between fires which burned someplace in a particular-sized unit of the forest, such as a drainage, but not necessarily involving the same point" (Kilgore and Taylor 1979). The importance of this distinction is that "frequency" reflects fuel, climatic, and ignition factors inherent in the ecosystem or forest type, while "fire incidence" also is affected by the size of the area being observed. Thus in a study of a giant sequoia (*Sequoiadendron giganteum*)--mixed conifer forest, the patchy fire regime was recorded every 17-23 years on individual trees, every 9-17 years in 1- to 2-acre (0.4- to 0.8-ha) clusters, every 5-9 years somewhere in 40-acre (16-ha) study sites, and every 2 years somewhere in 2,500-acre (1 000-ha) drainage (Kilgore and Taylor 1979). Obviously, the larger the unit size, the greater the numbers of fires and the shorter the intervals between them without any basic change in ecosystem function. By contrast, where fires are generally extensive, as in chaparral, recurrence intervals would often be similar for both single-acre and 100-acre or larger units. Hence, fire incidence alone is an incomplete description of the fire regime of a forest and a far less useful measure than either "fire frequency" or "fire cycle."

In discussing fire's role in the evolution of plant attributes, Keeley (1979) has pointed out that for that purpose, a "natural" fire frequency should include only lightning ignitions. For other purposes, such a distinction may be unnecessary. In any case, with the exception of sequoia-mixed conifer forest (Kilgore and Taylor 1979), there is little quantitative data upon which to base judgment of what proportion of presettlement ignitions were started by lightning or aboriginal sources. Hence, in this paper, I will not attempt to separate these two sources of ignition, although aboriginal burning was clearly significant in certain ponderosa pine and giant sequoia forests, and perhaps in other vegetation types as well.

Most studies of fire history and fire ecology of certain forest types specify intensity (if at all) in subjective and nebulous terminology such as "cool/light" or "hot/severe." Use of categories such as (1) low-intensity surface fires, (2) medium to high-intensity surface fires (torching), and (3) high-intensity crown fires is preferable, provided a range of fire intensity is noted for each class. Sando (1978) has suggested use of intensities greater than 1200 Btu/ft/sec to separate high-intensity fires from low- to moderate-intensity fires. Ecologists often appear to lack a clear understanding of fire behavior and its importance to the sound interpretations of fire effects (Van Wagner and Methven 1978). So it is not yet possible to relate quantitative intensity measurements, such as heat production per second per unit length of fire front (Byram 1959, Van Wagner 1965, Albini 1976), to specific changes in the ecosystem. Part of the past disagreements about the role of fire in a given forest or habitat type can probably be attributed to this lack of data refinement and documentation (Kilgore 1973b). Future field and laboratory studies must strive to resolve this problem by correlating fire effects with fuel, fire behavior, and environmental parameters.

FREQUENT, LOW-INTENSITY SURFACE FIRES

Frequent, low-intensity surface fires were characteristic of presettlement ponderosa pine (Pinus ponderosa) and giant sequoia-mixed conifer forests (Weaver 1951, Cooper 1960, Biswell 1967, Kilgore and Taylor 1979). Even certain Douglas-fir and western larch (Larix occidentalis) forests in the Rocky Mountains were kept open for centuries by such frequent natural burning (Arno 1980) along with insect epidemics and other mortality factors.

In his summary of the effects of fire on western forests, Weaver (1974) quoted a number of early explorers who, in describing the forest structure of Sierra Nevada montane forests, referred to "the inviting openness of the Sierra woods...trees of all species standing more or less apart in groves, or in small, irregular groups...with openings that have a smooth, parklike surface, strewn with brown needles and burs" (Muir 1894). One even spoke of being able to ride their horses "at a free gallup through the forest" which seemed like a vast covered hall where "in stately groups, stand tall shafts of pine" (King 1871). Although these statements reflect what we think sizable portions of these patchy forests were like, we should be cautious in extending these specific comments to imply that all areas of these forests were this open at all times.

One of these same early-day observers (Muir 1901) described the intensity of a fire he saw in 1875 in what is now Sequoia National Park, Calif., which resulted from this open type of structure and contrasted it with the intensity found in the dense chaparral scrubland and in certain dense forests of the Rocky Mountains and the Cascades:

The fire came racing up the steep, chaparral-covered slopes... in a broad cataract of flames.... But as soon as the deep forest was reached, the ungovernable flood became calm, like a torrent entering a lake, creeping and spreading beneath the trees.... There was no danger of being chased and hemmed in, for in the main forest

belt of the Sierra, even when swift winds are blowing, fires seldom or never sweep over the trees in broad, all-embracing sheets as they do in the dense Rocky Mountain woods and in those of the Cascade Mountains of Oregon and Washington. Here they creep from tree to tree ...allowing close observation....

The presettlement structure of pine and mixed conifer forests in the Sierra Nevada and intensity of fire which is possible because of that structure was described by Show and Kotok in 1924:

The virgin forest is uneven-aged, or at best even-aged by small groups, and is patchy and broken; hence it is fairly immune from extensive, devastating crown fires. Extensive crown fires, though common in the forests of the western white pine region, are almost unknown in the California pine region. Local crown fires may extend over a few hundred acres, but the stands in general are so uneven-aged and broken and have such a varied cover type that a continuous crown fire is practically impossible.

Ponderosa Pine Forests

Average fire frequencies in presettlement ponderosa pine forest varied from 6 to 19 years in different parts of its range (Wright 1978), with 5 to 12 years found in Arizona and New Mexico (Weaver 1951), 8 to 10 years being characteristic of ponderosa pine in California (Show and Kotok 1924, Wagner 1961, McBride and Laven 1976); 8 to 18 years in various parts of Oregon and Washington (Keen 1940; Weaver 1955, 1959; Soeriaatmadja 1966; Hall 1976); and 6 to 10 years reported from the Bitterroot National Forest in Idaho and Montana (Arno 1980). In forests containing a mixture of ponderosa pine and white fir (Abies concolor) in southern Oregon, McNeil and Zobel (1979) found mean intervals between fires that varied from 9 to 42 years at given sites.

Early studies of stand development in ponderosa pine by Weaver (1943, 1967) and Cooper (1960, 1961) help interpret structural changes with fire exclusion. In Arizona ponderosa pine forests, Cooper (1960) noted that under presettlement conditions, low-intensity surface fires, set by lightning or Indians, burned through the forest at regular intervals of 3 to 10 years. These fires served as thinning agents and played an important role in the cyclical process of stand development.

In describing a simplified form of this process, Weaver (1967) stated: "Periodic burning causes development of uneven-aged stands, comprised of even-aged groups of trees of various age classes." The system operated because low-intensity fire killed more small pines under canopies of larger trees than in openings. It did so because a surface fire would burn with greater intensity through heavy accumulations of flammable needles, cones, and bark scales which build up under larger trees than in the lighter and often less continuous fuels in the openings. But at various sites throughout the forest, even-aged groups of trees were killed by insects, disease, lightning, or windthrow. These groups of dead trees were gradually reduced to ashes in subsequent fires, leaving openings in the forest canopy within which pine seeds could germinate and young pines survive. (Another possibility would be that fire by chance would miss certain sites and allow enough fuel buildup that overstory trees would be killed in subsequent fires, leading to an opening.) Within such openings, the small accumulation of needles from these newly established young pines would not support a surface fire, although dry grasses and forbs in the openings would. Hence, until the pines were large enough to build up fuels beneath their own canopy, fires were not intense enough to kill them; and by the time they did contribute such heavier fuels, many of them were large enough to survive the low-intensity surface fires.

Cooper (1961) found that ponderosa pine forests in northern Arizona have a relatively simple species composition, yet a complex spatial structure. Several types of pattern or "scales of pattern" were identified, ranging from (1) a large-scale pattern of differences in density, growth, and species composition induced by local variations in topography and soils, through (2) a patchy mosaic pattern of even-aged groups averaging about 0.2 acre (0.1 ha) in size and maintained largely by fire, to (3) variations in stand density within a single even-aged group, primarily due to chance factors in early stand development. Cooper (1961) concluded that, "The clearly identifiable pattern in ponderosa pine forest is the result of the intolerance of the species to shade, the harsh environment which restricts the number of species present, and periodic natural fires...."

Since settlement of much of the West between 1850 and 1900 and the developing policy of fire exclusion, major changes in fire frequency and intensity have taken place. Cooper (1960, 1961) reported that in the absence of frequent, low-intensity fires, dense sapling thickets of young pine have covered the region. This has caused major changes in vegetation structure from the all-aged forest made up of even-aged groups with no understory saplings found under presettlement conditions. By comparing an area typical of presettlement conditions (where natural fires have continued over the years) with two areas typical of present conditions (fire exclusion), Cooper (1960) found that the major decrease in fire frequency had resulted in (1) diameter distributions in young even-aged stands which are skewed toward smaller trees; (2) stagnation of growth in the young pine in stands where density exceeds 6,000 stems per acre (14 800 stems per ha); (3) a less distinct patchwork pattern of reproduction than found in burned forests; (4) many more trees per acre; and (5) more saplings beneath mature trees. In turn, this change in structure as a result of long continued fire exclusion has increased the likelihood of high-intensity wildfire "by permitting excessive buildup of dry fuel on the forest floor, by leaving the tree crown level near the ground where ignition of live needles is more likely, and by permitting the formation of dense uninterrupted sapling stands over wide areas" (Cooper 1960).

Weaver (1947) made a similar comparison between two 40-year-old ponderosa pine stands, one burned and one unburned on the Colville Indian Reservation in Washington. He found the burned area was composed of 1,100 young trees per acre (2 717/ha), on the area stocked) and the trees averaged 7.4 inches (18.8 cm) diameter and 32.2 ft (9.8 m) in height. The unburned area had 14,800 young trees per acre (36 556/ha) averaging 1.7 inches (4.3 cm) diameter and 12.3 ft (3.7 m) in height.

Giant Sequoia-Mixed Conifer Forests

Similar changes were taking place in the sequoia-mixed conifer forests. In presettlement times, low- to moderate-intensity surface fires burned through giant sequoia-mixed conifer forests every 9 to 16 years, killing many young white fir while they were still part of the understory level of vegetation and fuels (Kilgore and Taylor 1979). Intense stand-replacing fires were apparently not part of the history of sequoias in Kings Canyon National Park, Calif., during the past 400 to 2,000 years.

With the elimination of aboriginal burning in the late 1800's and ever more effective fire suppression in the early 1900's, an increasingly dense understory of shade tolerant species such as white fir and incense-cedar (Calocedrus decurrens) developed beneath the canopy of Sierra Nevada mixed conifer forests (Kilgore and Taylor 1979, Parsons and DeBenedetti 1979). This altered considerably the nearly crown-fireproof structure of the presettlement forest (Kilgore and Sando 1975). Even in 1924, Shaw and Kotok found that structural changes had occurred which affected the intensity of fire likely in these forests:

Existing second-growth stands are typically even-aged and fully stocked, have a continuous, unbroken canopy, and are consequently susceptible to the most destructive type of forest fire. To those familiar with the occurrence of crown fires in the dense, even-aged forest of western white pine and Douglas-fir in the Pacific Northwest, a field examination of the second-growth western yellow pine forests of California would be immediately convincing that these stands also represent an exceedingly high inherent hazard and that this hazard differs from that of the virgin forest.

Since that time, increasing numbers of studies have been undertaken aimed at understanding the role of fire in montane vegetation of the Sierra Nevada and particularly the giant sequoia-mixed conifer forest (Biswell 1961, 1967; Hartesveldt 1964; Hartesveldt and Harvey 1967; van Wagtendonk 1972, 1974; Agee 1973; Kilgore 1973a, 1973b; Weaver 1974; Bonnicksen 1975; Kilgore and Sando 1975; Parsons 1976, 1977, 1978; Agee and others 1978; Bonnicksen and Stone 1978; Harvey and others 1979; Kilgore and Taylor 1979). Although few of these studies have dealt in a comprehensive way with the impact of fire on the various aspects of forest structure, a number of them yield valuable interpretations of the impact of changes in frequency and intensity of fire on species composition, age structure, horizontal arrangement, and vertical stratification.

The recent studies by Bonnicksen (1975) and Bonnicksen and Stone (1978) are the most specific efforts to understand the relationship between fire frequency and detailed forest structure in a giant sequoia-mixed conifer ecosystem. Bonnicksen and Stone (1978) have sought to (1) characterize quantitatively the structural properties of the presettlement giant sequoia-mixed conifer forest using both early descriptions and an analysis of existing vegetation; (2) characterize the dynamic properties of the forest and the processes which brought about changes in forest structure prior to the influence of European man; (3) document quantitatively the structural changes which have occurred as a result of the fire exclusion policy; and (4) develop quantitative guidelines for reconstructing alternative approximations of the presettlement forest structure.

Like Cooper's (1960) and Weaver's (1943) perception of ponderosa pine forests, and Stone (1978) perceive the giant sequoia-mixed conifer forest as a "mosaic of aggregations." And as in the case of ponderosa pine forests, disturbances such as fire, lightning, windthrow, and insects and disease infestations occur in small areas and produce openings or "gaps" in the forest. This occurs in part because fire often burns in a highly variable pattern of intensities in these forests, as well as in ponderosa pine and most other Sierra Nevada forests. It may burn with high intensity in one site, with low intensity nearby, and not at all in another site, with great variations in temperature and energy output over short horizontal and vertical distances, often related to localized accumulations of fuels. Surface temperatures, as an example, can vary from 204° to 648° C or more with no uniformity of distribution in a given burn (Kilgore 1973a, 1973b).

Once a gap has been created, species which can successfully seed into the opening and survive do so, forming an even-aged patch. If there is no further disturbance, shade tolerant species will begin to grow in the understory, producing several layers, each relatively even-aged. "The result of the gap formation process is a forest that can best be described as a mosaic of groups of trees, or aggregations, which can differ from one another in their age, the number of their vertical layers or tiers, and their species composition" (Bonnicksen and Stone 1978). A primary concern of this paper is the impact of fire frequency and intensity on these three variables and the role of fire in maintaining the distinction between adjacent aggregations.

The main structural changes in the giant sequoia-mixed conifer forests in the absence of surface fires have been (1) a large increase in the younger age classes of shade tolerant white fir in all parts of the forest (Kilgore 1973a) with a corresponding decrease in young, fire-dependent ponderosa pine, black oak (*Quercus kelloggii*), and giant sequoia (Parsons and DeBenedetti 1979); (2) a smaller increase in young sugar pine (*Pinus lambertiana*); (3) the survival of one or more vertical layers or tiers of white fir beneath (or perhaps in aggregations adjacent to) the overstory canopy of sequoia and pine; (4) a denser forest generally, particularly of young white fir (Parsons and DeBenedetti 1979), with 1,500 stems of various mixed-conifer species per acre found in some areas (Kilgore 1973a); and (5) a blending of what had been discrete patchy units into a more uniform forest, with more uniform burning intensities, "... gradually destroying the identity of the individual aggregations of trees and shrubs that were so readily seen in presettlement times" (Bonnicksen and Stone 1978).

The most conspicuous change found by Bonnicksen and Stone (1978) in overstory structure of a giant sequoia-mixed conifer forest was the general increase in area dominated by aggregations of pole-sized and mature conifers and a decrease in area occupied by aggregations of sapling- and seedling-sized trees, shrubs, grasses, and forbs. In the 87 years between 1890 and 1977, they found the acreage covered by these older age classes of white fir had more than doubled and there was a corresponding decrease in younger age classes as well as a decline in aggregations of black oak and shrubs. The decline of aggregations dominated by small fir, black oak, and shrubs can be considered a logical result of small fir growing larger combined with fewer gaps in the forest and hence fewer opportunities for young trees and shade intolerant shrubs to become established and survive.

Changes in understory vegetation have also occurred. In presettlement times, according to Bonnicksen and Stone (1978), nearly half of the understory vegetation in the watershed was made up of seedlings, shrubs, and forbs or there was bare soil and rock with no understory. When this was combined with mature and pole-sized aggregations lacking any understory and with aggregations of low stature vegetation, nearly 75 percent of the watershed apparently had the fairly open appearance described in historic accounts. In the absence of fire, however, there has been more than a 300 percent increase in aggregations of pole-sized conifers with an understory of saplings or seedlings.

These changes in structure of both top tier and understory forest aggregations also have an impact on the quantity and arrangement of fuels that accumulate and, as such, on the potential intensity of fire. Without frequent low-intensity surface fires, shade tolerant white fir, with its low-hanging branches from the various age classes of seedling, sapling, and pole-sized trees, forms an almost continuous fuel supply from ground level to their tops 10 to 100 ft (3 to 30 m) or more in height (Kilgore and Sando 1975). The larger fir, in turn, frequently reach the lower crowns of mature trees. This staircase structure of age classes in the forest forms a ladder-like arrangement of fuels with a high potential for fire to pass from surface fuels into giant sequoia crowns.

Kilgore and Sando (1975) concluded that low to moderate-intensity prescribed burning in a particular giant sequoia-mixed conifer forest modified the structure of the lower layers of the forest in such a way that the potential for high-intensity surface fires was substantially reduced. This was accomplished by reducing surface fuels and crown fuels in the lower 55 ft (16.8 m) of the forest and by increasing the mean height of the base of the crown from 3 to 16 ft (0.9 to 4.9 m).

Localized, high-intensity surface fires, however, were probably also both a natural part of presettlement forests (Bonnicksen 1975) and necessary for survival of giant sequoia seedlings (Harvey and others 1979). As such, fire intensity can have

considerable impact on postfire species composition. Following another prescribed burn, Kilgore and Biswell (1971) found the greatest number of giant sequoia seedlings on plots with the most intense burning conditions. They believed that the intensity of fire created a rising convection column of heat which not only dried out and killed needles more than 100 ft (30 m) up in several giant sequoia trees, but also caused drying out and opening of giant sequoia cones and thus contributed to very heavy seed fall in the area of the hottest burn.

Whereas the lightweight giant sequoia seeds germinate readily in the soft, friable, ashy soil which is provided after most fires, Harvey and others (1979) found the survival rate of seedlings in soils subjected to high-intensity burns was 10 times that of seedlings on other substrates. Because of its great longevity, however, few surviving giant sequoia seedlings are required in each fire cycle to perpetuate the natural structure of the ecosystem.

Bonnicksen and Stone (1978) believed that prescribed burning alone would not restore presettlement conditions to the giant sequoia-mixed conifer forest. They contended that because fuels have accumulated to such an extent, the numbers of sites subjected to high-intensity fire will be larger than would be expected under presettlement conditions. Hence, understory saplings would be reduced in all aggregations, even those in openings needed to start new age classes of white fir. In addition, they felt that the high intensities reached by many prescribed fires will lead to relatively uniform site conditions and to reproduction that may also be more uniformly dispersed than might be desired.

Compensating for the present structural changes in the forest will now be particularly difficult because the larger white fir (with thick bark) are much less likely to be killed by moderate fires, and any higher intensity fires may also kill both sugar pine and giant sequoia (Kilgore 1973b). Some fairly sophisticated and expensive forest manipulation techniques--perhaps including cutting some sizable fir and protecting certain aggregations of small fir--may need to be used to restore the forest to what we believe were more natural environmental conditions.

INFREQUENT, LOW-INTENSITY SURFACE FIRES

Sierra Nevada Subalpine Forests

Fires in subalpine forests of whitebark pine (Pinus albicaulis), red fir (Abies magnifica), and lodgepole pine in the Sierra Nevada behave differently from fires burning in lower elevations or in areas with different topography, forest composition, fuels, and rockiness. They commonly spread slowly or not at all, they rarely burn the crowns and kill overstory trees, and they are generally less intense than fires in montane forests of the Rocky Mountains or Cascades (Kilgore and Briggs 1972). Such high-elevation areas often have many natural firebreaks such as sparsely vegetated ridges, barren rocky areas, and streams and draws with relatively fire-resistant riparian vegetation.

In studies of a prescribed burn in 1968 in a forest of red fir and lodgepole pine, many mature lodgepole pine were readily killed by the fire, while germination of lodgepole seedlings was stimulated (Kilgore 1971). Few older red fir were affected by the fire, but many fir saplings and seedlings were killed, resulting in decreased coverage by fir thickets. The intensity of the fire was considerably lower than fire in the drier, heavier fuel conditions which are presently found in lower-elevation, postsettlement mixed conifer forest. There was little evidence of fire entering the crowns; whereas the crowns of some individual trees with sufficient fuels accumulated at their base did ignite, the fire did not spread to adjacent trees.

During the course of its program of allowing natural fires to burn, the National Park Service has monitored a number of fires in these subalpine zones and found that most lightning fires are less than an acre in size and burn only a few days. Several fires, however, burned considerable acreage over several months' time, but none burned intensely over large areas or became a control problem (van Wagtendonk 1977; Parsons 1977, 1979).

We are not sure just how frequent these fires were in presettlement times. With the shorter growing season in these higher elevations, it is estimated that fuel accumulation would be small enough each year that fire frequencies and intensities would be much less than that found in lower elevation montane forests (Kilgore 1971). Despite their relatively low intensity and infrequent occurrence, fires in these subalpine types played important roles. Because of long life spans and slow growth, however, they need not occur often to be a controlling factor.

Rocky Mountain Subalpine Forests

Whereas high-intensity fires have clearly been part of the spectrum of fires found in lower subalpine forests in the Rocky Mountains, Arno (1976) concluded that because of moist, sparse fuels in the upper subalpine forest, fires are much less frequent and intense. Sneek (1977) quoted a report from Glacier National Park, Mont. indicating that fires at higher elevations (over 5,000 ft or 2 000 m) are rarely extensive and are infrequent, perhaps every 300 to 600 years. Tande (1977) reported a mean fire return interval of 74 years for 124-acre (50-ha) blocks of subalpine forest in Jasper National Park, Alberta.

Gabriel (1976) found that fires in the subalpine fir zone occurred in a random pattern, with scars on adjacent trees often from different years. This apparently resulted from a high incidence of lightning fires with a low volume of fuel and open stands. Romme (1977) pointed out that a reduced frequency of fire in high-elevation spruce-fir forests of the Medicine Bow Mountains of Wyoming may result from the long-lying snowdrifts and frequent summer rain showers found in these Rocky Mountain subalpine forests.

INFREQUENT, HIGH-INTENSITY SURFACE FIRES

Redwood Forests

The natural fires in coast redwoods (Sequoia sempervirens) were probably infrequent, intense surface fires (Heinselman 1978). Few studies, however, have been done on fire frequency in this type. In work with more than 100 stumps on a 30-acre (12-ha) site in Humboldt County, Calif., Fritz (1932) concluded that there had been at least 45 severe fires in that locality during the past 1,100 years or about four fires per century.

McBride and Jacobs (1978) found intervals of 21.7 and 27.3 years between fires on 42 stumps found in two sites near Muir Woods National Monument in Marin County, Calif., and "intervals as short as 4 or 5 years on some stumps were not uncommon." In the absence of fire since the early 19th century, a buildup of both surface and ladder-like vertical fuels has occurred, which results in: (1) low-to-medium fire hazard in surface fuels, with some higher hazards in young redwood and Douglas-fir/hardwood types; and (2) fairly high fire hazard in ladder fuels, particularly in the Douglas-fir/brush and hardwood types and the redwood/hardwood types (McBride and Jacobs 1978).

Stone and others (1972) believe redwoods are seral and strongly dependent on fire and flooding for their perpetuation. Franklin and Dyrness (1973) concur in this, based on massive fire scars on almost all large redwoods in one area. Others feel the species is climax because of its high shade tolerance (Waring, personal communication, as noted in Franklin and Dyrness 1973). In his work in the northern range of the redwoods, Steve Veirs (personal communication) at Redwood National Park has identified

patterns of establishment of Douglas-fir (Pseudotsuga menziesii) in redwood stands at 200- to 500-year intervals on mesic sites, presumably related to infrequent, high-intensity surface fires. Inland, on higher, drier sites, redwood dominance is reduced and Douglas-fir age classes suggest a return interval of 50 to 100 years for fires which open the forest canopy to the extent necessary for fir establishment. In its northern range, redwood appears to reproduce at replacement rates (about 1 tree/acre every 50 years) in the absence of fire. With the exception of Douglas-fir, associated trees such as tanoak (Lithocarpus densiflora), hemlock (Tsuga heterophylla), and grand fir (Abies grandis), like redwood, appear to reproduce successfully both with and without ground fires.

SHORT RETURN INTERVAL, STAND-REPLACEMENT FIRES

Chaparral and quaking aspen (Populus tremuloides) are two vegetation types which illustrate a short return interval between stand replacement fires. Both forms have all aboveground vegetation killed by periodic, intense burning--either crown fire or high-intensity surface fires, but each survives by sprouting from root crowns or by reseedling. In addition, several types of woodland and scrub vegetation are prevented from invading grasslands by periodic crown fires. Pinyon-juniper and sagebrush scrub illustrate this response.

Chaparral

Large sections of chaparral are found in California and Arizona, often occurring as a band of vegetation between grasslands below and forests above. In California alone, it covers 11 million acres (4.5 million ha) (Bentley 1967). Chaparral is best developed or most extensively distributed on the steep slopes and shallow soils of southern California (Menke and Villasenor 1977).

Slope aspect is an important factor in the chaparral environment, in part determining which species make up a local chaparral community and even succession following fire (Hanes 1971). Chamise (Adenostema fasciculatum) is a prominent member of the climax chaparral, often forming almost pure stands in some areas. Other sites are dominated by various species of manzanita (Arctostaphylos spp.), ceanothus (Ceanothus spp.), and scrub oak (Quercus spp.). Species of the latter three genera also make up much of the patches of chaparral that occur within conifer forests (Biswell 1974).

Recent work by Byrne (1978) provides evidence that wildfires were an important part of the California chaparral environment long before European man arrived on the scene. Using data gathered from ancient charcoal fragments deposited in marine sediments between 1400 and 1550 A.D., Byrne's (1978) preliminary conclusions were that prehistoric fires in chaparral and woodland of the Los Padres National Forest area of southern California "occurred less frequently than during the modern period, but those that did occur were of greater intensity and aerial extent. We estimate the recurrence interval of these fires to be anywhere from 20 to 40 years."

Fire has likely been an important factor in chaparral for a long time. The plant species involved have developed two main strategies for surviving burning: many species exhibit vigorous sprouting ability following fire; others have seedcoats that are altered by fire, and thus germination of seeds is favored.

Present frequencies of fire in this type of scrubland are reported to vary from less than 10 years in sections of the south coastal region of California through 20 to 25 years in the north coastal regions to as much as 50 to 100 years in manzanita chaparral growing at 4,000 ft (1 220 m) elevations on northern slopes.^{1/} Under fire

^{1/} Material in preparation for a textbook on fire ecology by Henry A. Wright and Arthur W. Bailey.

suppression conditions today, many areas have not burned for 60 to 100 years. Based on work in Sequoia National Park, Calif., Parsons (1976) concluded that chamise regained much of its prefire structure within 14 years, and that by 35 years, "...it shows all the characteristics of a mature stand, most of the successional subshrub forms having disappeared."

The dramatic impact of interaction between fire frequencies and intensities on the one hand and vegetation structure and reproductive strategies on the other is illustrated by recent work in southern California chaparral. Keeley and Zedler (1978) believe chaparral is adapted to both short and long fire-free intervals, a reflection of the unpredictability of fire in that environment. They suggest a model which includes both (1) a short fire cycle which favors sprouting shrubs over those reproducing entirely from seed; and (2) a long fire cycle in which "sprouters" and "seeders" coexist. In the short cycle (25 years), there are fewer dead shrubs before the fire, more potential resprouts, less intense fires, lower fire-caused mortality of sprouting shrubs, and smaller openings for seedlings. In the long cycle (100 years), however, there are more dead shrubs before the fire, fewer potential resprouts, higher intensity fires, more fire-caused mortality of sprouting shrubs, and larger openings for seedlings. They predict that with the present fire cycle of every 20 to 30 years, both sprouting and seedling species regenerate but, over long periods of time, sprouting species may gain an advantage.

Keeley (1977) believes that southern California chaparral may have evolved under relatively long fire-free intervals. Similar conclusions were reached by Sauer (1977) who suggested that chaparral of the Santa Monica Mountains evidently "was adapted to a regime of infrequent, large, intense, nonselective fires, which has not been substantially altered by man." Evidence of this was presented by Byrne and others (1977).

In the case of the chaparral adjacent to conifer forest in Sequoia National Park, Parsons (1976) believed that fire prevention and suppression have led to the "formation of an unnatural, highly flammable, nearly uniform, old-aged...brush community." He was concerned that with the known high frequency of lightning fires in the area and increasing recreational use, an unnaturally intense fire would both destroy the vegetation mosaic that currently exists and threaten the nearby groves of giant sequoia.

Parsons (1976) indicated that existing fuel accumulations need to be reduced so that more natural fires could be allowed to burn at frequent intervals. Once fire has restored a natural mosaic of age classes and community types, "these age-class boundaries would then function, along with topographic features, as natural fuel breaks for limiting the size of future fires and thus perpetuating the mosaic" (Parsons 1976). Philpot (1977) shares the same concern that without fire for periods of 50 years or longer, age-class boundaries become less distinct and chances increase for larger, more catastrophic fires. Byrne and others (1977), however, believe that some presettlement fires were large and catastrophic.

Quaking Aspen

Studies by Loope and Gruell (1973) indicate that in presettlement times successful regeneration of aspen stands was stimulated by fire. Hendricksen (1972) hypothesized fire frequencies of 50 to 100 years for aspen. Loope (1971) noted that while occasional aspen may live to 200 years in the absence of intense fire, they tend to deteriorate after 80 to 100 years and be replaced by conifers. This is true because aspen is fairly short-lived, is susceptible to many diseases, and cannot survive or reproduce in the shade of competing conifers such as Douglas-fir (Loope 1971, Gruell and Loope 1974). Although the aboveground portion of aspen is easily killed by fire, its root system is rarely damaged; hence aspen clones are perpetuated by fire, and aspen gets a headstart on competing conifers by root sprouting.

Clements (1910) found that aspen sprouts grew more rapidly after an intense fire than after a light fire. Horton and Hopkins (1966) also found that a fire intense enough to kill all aspen stems and remove litter and duff is desirable to produce prolific suckering, whereas low-intensity fire does not achieve this result. Gruell and Loope (1974) concluded that fire suppression during the past 50 to 70 years is a major factor contributing to the recent decline of aspen in Jackson Hole, Wyo.

Pinyon-Juniper Woodland

The pinyon-juniper association covers more than 43 million acres (17 million ha) in western North America (Wright and others 1979). Before livestock grazing was involved, fire, drought, and competition with grass jointly limited the distribution of juniper (Juniperus occidentalis).

Buckhardt and Tisdale (1976) report presettlement intervals between fires in western juniper stands in southwest Idaho comparable to the 13- to 18-year interval found by Keen (1940) for ponderosa pine forests. Such frequent fires kept junipers restricted to shallow, rocky soils and rough topography in many parts of the West. With initiation of livestock grazing, reduced competition from grasses has permitted pinyon (Pinus edulis) and juniper to invade adjacent grass and sagebrush communities; with reduced numbers of fires and lower intensity burning (without grass fuels), the juniper invasion has continued unchecked (Martin 1978, Wright and others 1979). In a study of two species of mistletoe that infest pinyon and juniper in Grand Canyon National Park, Ariz., Hreha (1978) found that fire was the most limiting factor on the mistletoe, and that the mistletoes and their hosts appeared to be in equilibrium.

Along the uplands in Mesa Verda National Park, Erdman (1970) found that recurrent fires had maintained a Gambel oak (Quercus gambelii)-serviceberry (Amelanchier utahensis) mountain brush vegetation as a fire climax. But under fire suppression policies, pinyon-juniper forest is gradually replacing the extensive shrub vegetation. Prescribed fire will kill pinyon and juniper less than 4 ft (1.2 m) tall (Wright and others 1979), but taller trees are more difficult to kill. Hence, to prevent invasion of grass and shrublands by pinyon and juniper, reburns are needed at least every 20 to 40 years.

Sagebrush Scrub

Sagebrush-grass vegetation covers at least 96 million acres (40 million ha) in the western United States, mostly below the pinyon-juniper zone (Wright and others 1979). Big sagebrush (Artemisia tridentata) is the principal fuel for free-running fires in the broad Great Basin Desert ecosystem which covers much of Nevada, southern Oregon, southern Idaho, and parts of Wyoming, Utah, and Arizona (Humphrey 1974). In presettlement times, minimum fire frequency in this community in northern Yellowstone National Park was 32 to 70 years (Houston 1973), and Wright and others (1979) felt 50 years is likely.

There has been little research on effects of fire in the sagebrush desert, perhaps because fires are rarely extensive in the ecosystem (Humphrey 1974). However, this high, cold desert or sagebrush desert is more subject to burning than the hotter, drier, more southerly Mojave, Sonoran, and Chihuahuan Deserts. This is true in part because the higher elevations and greater moisture permit growth of fire-supporting grasses and forbs beneath and between the sagebrush (Humphrey 1974). In addition, there is considerable fuel from adjacent juniper, pinyon-juniper, or grassland vegetation types that carry fires from these areas into the sagebrush type.

Fires have a major impact on such nonsprouting shrubs as Artemisia tridentata within the sagebrush-grass community, but specific responses vary with seasonal timing, intensity, and frequency of burning (Wright and others 1979). In degraded

big sagebrush/Thurber needlegrass (Stipa thurberiana) rangeland communities, north of Reno, Nev., wildfires killed the sagebrush, stimulated sprouting of two native shrubs, and allowed downy brome (Bromus tectorum), an "alien" annual grass, to dominate the study areas (Young and Evans 1978). The annual grass appears to provide an accumulation of fine fuel that readily ignites and carries fire to the widely spaced sagebrush plants, thus setting in motion a cyclic phenomenon leading toward conversion to an annual grassland.

Artemisia tridentata produces a growth ring that can be counted to determine age of plant or plant community (Ferguson 1960). In a study of shrub age structures on a mule deer winter range in Colorado, Roughton (1972) found an unusually large number of Artemisia individuals in the 55- to 59-year age class. This either suggested that some major mortality factor such as fire had occurred at about the turn of the century and "the population had not yet returned to equilibrium" (Roughton 1972) or there have been 60 years of poor conditions for reproduction since then. Future studies using this shrub age-dating technique may allow determination of age structures for a shrub population and in turn an interpretation of successional status and variations from predicted sequences which may result in part from fire impacts.

From a land management standpoint, to keep sagebrush in check, "prescribed fire can be a useful tool in many big sagebrush...communities if the fires are carefully planned...fires should not be too frequent and should be planned in early spring or after late summer" (Wright and others 1979). Particular species responses to fire must be understood to achieve whatever objective the land manager may have.

VARIABLE REGIME: FREQUENT, LOW-INTENSITY SURFACE FIRES
AND LONG RETURN INTERVAL, STAND-REPLACING FIRES

High-intensity, stand-replacing crown fires occur in various forest types in the West. In certain types, however, the fire regime varies between relatively frequent, low- to moderate-intensity surface fires and long return interval crown fires, depending upon weather conditions and ignition factors in particular sites. When wind and other weather conditions are favorable for intense burning, the likelihood of an ignition leading to a high-intensity crown fire depends on such forest structural factors as: (1) the spacing of trees; (2) the quantity of crowns per unit area; (3) the amount and arrangement of surface fuels; and (4) how high the crown canopy is above the surface fuel heat sources (Brown 1975). Such intense fires have occurred periodically at more than 100-year intervals in lodgepole pine, western white pine (Pinus monticola), and western larch forests of the Rocky Mountains and in Douglas-fir and lodgepole pine forests in the Cascades (Fahnestock 1977).

Wellner (1970) felt that the age structure of most Northern Rocky Mountain forests supported the conclusion that fire in this region tends to be catastrophic, killing most trees in the forest. Recent studies (based on fire-scar and stand-age data) summarized by Arno (1980), however, indicate that "historic fires occurred with vastly different frequencies and had markedly different effects in this region's diverse forest environments." In some habitats, fires maintained many-aged, open stands of seral trees, while in others, fires destroyed and replaced stands. This was true, Arno (1980) points out, because fires burned at variable intensities "...resulting in a mosaic of stands that differed in tree species composition and age-class structure."

One fairly consistent conclusion by scientists and resource managers working in most areas of the Northern Rocky Mountains seems to be that there are few areas in which shade tolerant, climax forests of spruce (Picea sp.), fir (Abies sp.), hemlock (Tsuga sp.), and redcedar (Thuja plicata) have been allowed to develop. Instead, fire--whether frequent and low intensity or less frequent and of higher intensity--has repeatedly favored the development of stands of intolerant, fire-dependent species

such as lodgepole pine, aspen, western larch, western white pine, ponderosa pine, and Douglas-fir (Wellner 1970, Habeck and Mutch 1973, Weaver 1974, and Arno 1980).

Most fires in the moist, north Pacific coastal forest were probably tiny and put out by rain. The larger fires, however, occurred infrequently, and with few exceptions were stand-replacing fires (Lotan and others 1981). Many fires in the Douglas-fir region of the Cascades were also of this type (Weaver 1974), although there is abundant evidence of low-intensity surface burning wherever ponderosa pine are found.

Lodgepole Pine Forests

The major vegetation pattern in lodgepole pine is caused by stand-replacement fires, although many uneven-aged lodgepole pine stands result from some lower intensity surface fires (Brown 1975). In a recent review of fire history in the Northern Rockies, Arno (1980) concluded that historic fire was rather frequent in communities dominated by lodgepole pine (25- to 50-year mean intervals in 100- to 200-acre (40- to 80-ha) stands where dry summers occur and 50- to 100-year intervals in such stands with wet summers). Brown (1975) concluded that average intervals between fires "for given localities" in this forest type vary from 60 to 500 years. Lodgepole, however, has a lifespan which varies with site and geographic location from 100 to 300 years or more, and tends to be eliminated from sites having a long interval between fires (Antos 1977).

Arno (1976) found evidence of low-intensity, creeping surface fires in lodgepole pine forests in some of his study areas in the Bitterroot National Forest of Montana. Loope and Gruell (1973) found similar evidence in lodgepole pine forests of north-western Wyoming. Gabriel (1976) also documented low-intensity surface fires at 20- to 40-year intervals in the southern part of his study area in the Bob Marshall Wilderness Area of Montana. He contrasted these with larger, stand-replacing fires that had burned much of the northern half of his study area. Even where these intense fires had burned, there were fire-scarred lodgepole pine and Douglas-fir, suggesting a sporadic pattern of lower intensity burning during relatively high-intensity fires.

The intensity and frequency of fires in lodgepole pine largely determine establishment of seedlings and subsequent development of stand density, age structure, and composition (Brown 1975). Higher intensity fires tend to favor lodgepole pine over such species as Douglas-fir and western larch, depending upon the local winds, topography, and fuels. In some instances, frequent fire may prevent lodgepole from invading aspen where the two grow in mixed stands (Brown 1975), except where intense burns kill aspen roots. The timing of the fire also made a difference. Burns that preceded a good larch seed crop must have favored larch. It is harder to predict the species composition of a lodgepole pine-mixed conifer forest after a low-intensity fire (Brown 1975). In areas with low- to moderate-intensity fires, Ayres (1900) found the composition of regeneration was similar to that of the overstory.

The structure in a lodgepole pine forest is affected by such mortality factors as needle miner, bark beetle epidemics, mistletoe infestations, and death of suppressed trees in the understory of a dense forest. These factors provide for a buildup of surface fuels that increase the probability of large, high-intensity fires (Brown 1975). Conversely, Gabriel (1976) found areas in the Bob Marshall Wilderness of Montana where a series of intense fires had modified structure and species composition in a way which prevented additional intense fires for a number of years. Muraro (1971) reported a similar situation where "a natural process of fuel modification by fire intensity may discourage second fires of high intensity on severely burned areas" This apparently happened because fires had consumed the heavy fuel loads and broken the continuity of fuels from ground to overstory crown in a way that resulted in relatively clean stands of healthy, thinned lodgepole pine; it will be many years before these stands will reach mortality age, break up, and change structure so that high intensity fires can be carried through again.

When aspen is not present, a second burn in less than 25 years may not allow time for lodgepole pine seed to be produced; hence, too frequent fires can create brushfields which remain for long periods (Ayers 1900, Wellner 1970). Low-intensity surface fires on the other hand sometimes remove spruce and fir from the understory and enable lodgepole pine to remain in nearly pure stands even when intermediate in succession (Gabriel 1976).

Douglas-fir Forests

Douglas-fir is widely distributed in the West, ranging from relatively dry forest with ponderosa pine, where it assumes a more shade tolerant climax role, to more moist forests with hemlock, cedar, and fir, where it assumes a more intolerant seral role. In the Pacific Northwest, it is a particularly prominent component of the timbered ecosystems of western Oregon and Washington between the subalpine forests of fir and mountain hemlock (*Tsuga mertensiana*) near the Cascade crest to the narrow band of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) along the coast (Weaver 1974). In much of this region, Douglas-fir is replaced by hemlock, cedar, and fir in the absence of fire. In the ponderosa pine region, however, Douglas-fir is the more shade tolerant species which dominates in the absence of fire (Weaver 1974). This is true because Douglas-fir is moderately tolerant, enduring more shade than ponderosa pine, sugar pine, western white pine, and lodgepole pine but less than western hemlock, western redcedar, and white and subalpine fir (*Abies lasiocarpa*). Douglas-fir needs mineral soil for germination of seeds and development of seedlings. While seedlings can become established under a closed canopy, they usually do not survive to become saplings without sunlight.

Frequencies and intensities of fires reported from Douglas-fir forests vary from (1) low- to medium-intensity surface fires at frequencies of 7 to 20 years in certain drier types in the Northern Rocky mountains (Houston 1973, Loope and Gruell 1973, Arno 1976, Tande 1977), through (2) moderate-intensity fires every 117 to 146 years in a more mesic situation in northern Montana (Sneck 1977), to (3) high-intensity crown fires reported in more mesic forests in many parts of the Rockies and the Pacific Northwest. The presence of Douglas-fir forest on a given site in the Pacific Northwest is considered by some authors to indicate periodic timber-killing fire (Martin and others 1976) at frequencies of 50 to 400 years. Evidence for such high-intensity crown fires in presettlement forest in the more mesic Douglas-fir region comes from reports by Issac and Muir, as quoted in Weaver (1974), that the first white men to arrive in these areas found extensive, immature, even-aged stands of Douglas-fir of the type that follow intensive fires. From his observations in the Puget Sound region in the late 1800's, Muir assumed these high-intensity crown fires had burned during rare drought conditions when such intense burning was possible. Under severe burning conditions, with strong winds, fires crowned in Douglas-fir and covered large areas, but otherwise were relatively low-intensity surface fires.

A history of repeated fires was common to all habitats supporting high populations of Douglas-fir in the coastal forests of British Columbia studied by Schmidt (1960). On Vancouver Island, nearly 2 million acres (0.8 million ha) of forest were burned between 300 and 400 years ago. Most of the mature Douglas-fir on the island owed their origin to very large fires which burned 310 and 410 years before studies by Schmidt (1970). Eight major forest fires burned this area between 150 and 1,100 years ago. The geographic range of coastal Douglas-fir, according to Schmidt (1960) is controlled "by low summer precipitation, high summer temperatures, and the frequency of severe summer lightning storms." He estimates that every 200 to 300 years for most coastal areas, these elements combine to set the stage for intense stand-replacing fires. The distribution of the species itself seems to be limited by incidence of forest fire; Douglas-fir are found on slopes of a U-shaped valley denuded by repeated fires in the past and on south-facing slopes with higher frequency of fires, while uneven-aged forests of more shade tolerant species are found on the more level plateau country and north-facing slopes where fires burn much less frequently.

Arno (1980) states that the major fires in the Northern Rocky Mountain Douglas-fir habitat types "...burned at different intensities in reaction to changes in stand structure, fuel loadings, topography, and weather. The result was a mosaic of fire treatments on the landscape, which tended to be self-perpetuating." Thus, frequent, low-intensity fires tend to keep stands relatively open, and the open structure, in turn, leads to low-intensity fires. On the other hand, high-intensity stand-replacing fires tended to lead to dense, pole-sized stands which are more susceptible to high-intensity crown fires.

Although small-sized, low- to moderate-intensity fires were characteristic of most of the Douglas-fir stands studied by Sneek (1977) in a small experimental forest in the Northern Rockies, she also found that intense, stand-replacing fires had killed much overstory vegetation in the mid-1800's on certain relatively dry, west-facing slopes. This led to regeneration by both Douglas-fir and lodgepole pine. Douglas-fir saplings are gradually replacing decadent members of the lodgepole pine overstory. In so doing, these saplings are creating a new, vertical forest structure which is ladder-like and hence more flammable. When combined with heavy standing and fallen lodgepole pine fuels, this modified vertical structure will support a stand-replacing fire.

Repeated burning or intense fires can eliminate Douglas-fir from some areas. Gabriel (1976) found that extensive areas in the drier southern half of his study area in the Bob Marshall Wilderness of Montana were changed from Douglas-fir to lodgepole pine by fires which burned the same sites in 1809, 1844-47, and 1889. On more moist sites in the northern half of his study area, he found that species composition changed from Douglas-fir and larch to lodgepole pine following particularly intense fires in 1889.

The decrease in fire frequency, which accompanied the beginning of effective fire suppression in the Bitterroot National Forest of Montana in 1920, has brought about major changes in the structure of many parts of the montane and subalpine forest. In drier habitat types, where Douglas-fir is the potential climax tree, dense understories have developed, "making a ladder of fuels that now endangers even the fire-resistant, old-growth overstory of ponderosa pine, Douglas-fir and western larch" (Arno 1976). Forest structure and fuel arrangement in the forest have also been altered by severe infestations of dwarf mistletoe (*Arceuthobium* spp.) in Douglas-fir, western larch, and lodgepole pine, at least partially the result of the decrease in fire frequency (Alexander and Hawksworth 1975). In some forest types, the consequent greater accumulation of fuels and the continuity of fuels over the landscape favor the development of high-intensity fires in areas where low- to moderate-intensity fires were found between 1735 and 1900 (Arno 1976).

In studies of the Selway-Bitterroot Wilderness in Montana, Habeck (1972) concluded that fire exclusion in the Douglas-fir zone has caused some major changes in the vegetational mosaic found prior to 1900. In those presettlement times, he feels, "the landscape would no doubt have exhibited a patchiness composed of contrasting life forms (blackened acres, brushfields, young conifer reproduction, and various seral and climax stands)." With fire suppression, however, diversity has been reduced and the forest has taken on a uniform appearance.

Other Types

The role of fire frequency and intensity is less clear for other species involved in the variable low-intensity surface fire/long return interval, crown-fire regime, such as the western larch and western white pine. Larch often occurs with Douglas-fir and ponderosa pine in certain sections of the Rockies and Cascades in Montana, Idaho, Washington, and Oregon (Sudworth 1908). Weaver (1974) indicated that larch is often associated with Douglas-fir in a mixed stand referred to as the "fir-larch" type, although nearly pure stands do sometimes occur. Unlike Douglas-fir,

larch is extremely intolerant of shade, and as such, its principal associate and competitor seems to be lodgepole pine.

Weaver (1974) quotes Sudworth as indicating that the composition of regeneration after burning depends upon which species releases its seeds first--larch or lodgepole pine. Gabriel (1976) and Antos (1977) note that within the shorter lifespan of lodgepole pine (100 to 250 years), stand-replacing fires increase the proportion of lodgepole pine in an area, whereas moderate-intensity fires favor western larch. However, on sites where lodgepole pine has been eliminated as a result of the long interval between fires, larch forms the dominant layer after intense fires as well (Antos 1977). This is true because even after 300 years without fire, large numbers of old-age larch remain which can serve as seed sources after an intense fire.

Daubenmire and Daubenmire (1968) reported that the proportion of larch commonly increases when fires follow one another within a few decades because this species has such thick bark that it is less susceptible than its associates to injury by surface fires. Gabriel (1976), on the other hand, found that too frequent fire around 1900 decimated larch populations within a portion of the Bob Marshall Wilderness. Antos (1977) noted that, "If lodgepole pine or western larch fail to establish after a fire, a mixture of Douglas-fir, grand fir (Abies grandis), western white pine, and spruce slowly form a new stand."

VERY LONG RETURN INTERVAL CROWN FIRES

The longer a forest stand goes without fire, the more the shade tolerant, climax species are favored over fire-dependent seral species. While some species like Douglas-fir can be seral in one forest type and climax in another, other species are nearly always climax, and seem to achieve dominance with very long intervals between fires. These include most of the spruces, true firs, western redcedar, and western hemlock. "As a general rule, the more shade tolerant the conifer, the greater is its susceptibility to damage and mortality from fire" (Lotan and others 1981). These species tend to occur on more moist sites, either (1) in higher elevations, as in the case of certain spruces and true firs; or (2) in sites more moist because of local topographic position; or (3) in sites which are more moist because of climatic conditions, such as the Pacific coastal forests of redcedar, hemlock, and certain other spruces and firs, or on the west slopes of the Northern Rockies in northern Idaho and western Montana, which are influenced by the prevailing winds and the Pacific maritime climate from the west.

In the absence of fire, the successional trend is toward increased dominance of true firs such as subalpine fir, grand fir, and white fir and a decrease in the spruces, Douglas-fir, and lodgepole pine. Because of the long natural interval between fires in these types, the suppression of fires for the last 50 to 75 years has probably had less impact on their structure than in areas of more frequent surface fires (Fahnestock 1976).

Spruce-Fir Forests

These forests are usually so damp they seldom burn (Weaver 1974) except during extreme droughts. During those periods, fires burn very intensely through these forests because their highly flammable green limbs are close to the ground. Intense burning in 350-year-old spruce-fir forests in Yellowstone National Park was apparently related to such forest structural factors as compact growth form, with numerous small branches close together, lower branches that do not self-prune, a fruticose lichen which had accumulated on the branches, and heavy accumulations of duff and rotten wood (Despain and Sellers 1977). Such an abundance of surface and ladder fuels led to a high probability of fire brands falling on fuels which would in turn produce flames reaching into flammable spruce-fir crowns.

Oosting and Reed (1952) quote Hansen's evidence that high-intensity forest fires have been a recurrent factor in the spruce-fir forests of the Medicine Bow Range of Wyoming during presettlement time. In the Bob Marshall Wilderness of Montana, Gabriel (1976) noted that periodic low-intensity fire prevented the growth of spruce and subalpine fir in stands of lodgepole pine.

In the Northern Rocky Mountains, Arno (1980) reported that moist subalpine fir-Engelmann spruce (Picea engelmannii) forests had fire-free intervals of 150 years or more, and that when fire did come, it was usually a high-intensity, stand-replacing fire. Sneek (1977) found spruce stands in moist draws that were 250 to 370 years old, with no evidence of fire.

Studies by Romme (1977) in the Medicine Bow Mountains of Wyoming indicate that topographic and microclimatic differences between canyon bottoms and adjacent slopes and ridges may result in differences in fire frequency and successional patterns following fire. Fires were less frequent in spruce-fir forests found along canyon bottoms than in adjacent upland lodgepole pine forest, and when fire did occur, succession to spruce-fir was more rapid and direct. "Thus, the pattern of canyon bottom spruce-fir forests surrounded by upland lodgepole pine forest is a result both of fewer fires and more rapid succession in the canyon bottom sites" (Romme 1977).

Hemlock-Cedar Forests

The extremely moist forest of western hemlock-western redcedar of the Northern Rocky Mountains and Sitka spruce-hemlock-redcedar of the Pacific coastal forests are discussed together here. Relatively little information on fire frequency and intensity is available on either of these types. In studies in the Selway-Bitterroot Wilderness of Idaho and Montana, Habeck (1976) noted that, "The oldest forest communities (over 400 years old), those burned least often, are those dominated by redcedar on the moist streamsides and in ravines." Hemlock-redcedar forests generally occur in sites with the dampest climate found in the Rocky Mountains, but extreme summer drought from time to time has set the stage for occasional, spectacular crown fires (Arno 1980). The most recent large conflagration was the 56,000-acre (22 672-ha) Sundance Fire in northern Idaho in 1967 (Anderson 1968), but earlier, high-intensity crown fires burned several million acres in 1889, 1910, 1919, 1926, and 1934, much of it in the hemlock and redcedar type of northern Idaho (Arno 1980). In some cases, the fuels generated by the first fires appeared to lead to a second burn which resulted in shrubfields taking over the site for decades.

The presence of cedar-hemlock forest on the western slope of the Olympics in Washington is interpreted by Martin and others (1976) as an indication of very long intervals between fires, more than 150 years. Lotan and others (1981) concluded that the wettest forest in this type may have burned at intervals of 500 years or longer.

True Fir Forests

High-intensity, stand-replacement fires at intervals of about 150 years were apparently more prevalent than surface fires in grand fir (Abies grandis) forests of Swan Valley, Mont. (Antos 1977). When such a fire occurs, grand fir and western redcedar, which developed below the canopy, are killed; the survival of a few seed trees or of viable seeds in burned cones is critical when large areas are burned (Lotan and others 1981). "Which species will attain the highest density is a function of seed source and the timing of good seed crops" (Antos 1977).

In the absence of fire, grand fir gains dominance over all other conifers in its habitat types as succession proceeds toward climax (Pfister and others 1977). Following fire, Douglas-fir, larch, spruce, and lodgepole pine on some sites invade along with grand fir, but by the time a pole-sized stand has developed, "Abies grandis is generally

the only species that continues to reproduce beneath the forest canopy" (Pfister and others 1977), with increased shade and soil moisture often playing important roles here. In the Selway-Bitterroot Wilderness of Montana, Habeck (1976) found that grand fir regeneration was spreading in all directions, into wetter, drier, and higher elevation sites. He concluded that expansion of the fire-sensitive grand fir may be a relatively new event related to fire suppression.

DISCUSSION

Gill (1979) noted that it is unfortunate when someone implies that either a wildfire or management fire will not harm vegetation because the flora is "adapted to fire." He points out rightly that this is an incomplete concept, and a better statement would be that, "the vegetation is adapted to a certain fire regime." The significance of this point is driven home by noting the broad range of frequencies and intensities which were found in presettlement forests and scrublands of the western United States, ranging from the frequent low-intensity surface fires of ponderosa pine to the very infrequent and high-intensity crown fires found in many spruce-fir forests. Frequent low-intensity burning would be just as out of place in spruce-fir forests as infrequent high-intensity crown fires are in naturally operating ponderosa pine ecosystems.

Yet, with fire having been suppressed in many western forests for the past 50 to 100 years, unnatural changes have been evolving slowly--even imperceptibly in some cases. This is leading to a sequence of events which may be developing for the first time ever. A conceptual model of this sequence of a sequoia-mixed conifer forest would show that suppression leading to longer intervals between fires would initially lead to increases in surface and crown fuels and to changes in the forest structure such that there would be (1) older age classes; (2) a denser forest (less openings); (3) a multilayered vertical structure; (4) an increase in ladder fuels; and (5) more shade tolerant species. This would next lead to increased probability of higher intensity surface fires with some individual tree crowns burning, and to sequential impacts on postfire forest structure, species composition, fuel accumulation, and both horizontal and vertical pattern. In turn, this would bring about changes in fire frequency and intensity. The unknown in such a model is how a new balance would be arrived at, as long as man puts substantial energy into fire suppression.

Such changes in the absence of fire during the past century or less are greatest in those forests which historically had a short return interval between fires and least in forests which had a very long return interval. For example, if the normal interval between fires is 300 years or more, the recent absence of fire for 50 to 100 years would be of little significance.

In certain northern forests, however, it appears that fire intensity is not a pure function of fuel buildup with age. Work by Van Wagner (1977) and Fahnestock (1977) suggests that crown fire potential is probably greatest at young and moderate age, then decreases as the stand matures. "Certainly the role of fire spread depends more on the quantity and arrangement of fire fuels than on the accumulation of downed logs" (Van Wagner 1978). Once breakup of the forest stand begins through death of certain older or weaker trees, there is a major increase in dead materials added to surface fuels and surface fire intensity might take a surge upward. Because of new openings in the crown canopy, however, continuous crown fires would then be less likely unless a well-defined conifer understory had arisen.

Plant Succession

Plant succession following fire does not necessarily follow a single pathway. As Cattellino and others (1979) point out, various species-specific attributes related to reproduction and survival determine the successional outcome when a given ecosystem is disturbed by fire. As an example, in the Northern Rocky Mountains, a community made

up of aspen, lodgepole pine, and western larch will have different outcomes depending upon the intervals between fires as they relate to the following life-history characteristics: (1) aspen's lifespan of 130 years and its vegetative reproduction; (2) lodgepole pine's lifespan of 250 years and its need for 20 years before mature cones are produced; and (3) larch's 300- to 400-year lifespan and its ability to disperse seeds widely from surrounding forests after a fire. If a community with aspen and lodgepole pine is burned less than 130 years after the last fire, both species will be present in the postfire succession. If the stand burns after 250 years, both species will be lost and larch will take over by seeding in from surrounding forests. If the stand burns in less than 20 years, lodgepole pine will be lost, but both aspen and larch would be part of postfire succession (Cattelino and others 1979). Thus, man-caused changes in fire frequency--through suppression or prescribed burning--can have major impact on the species composition and structure of a forest.

Insects, Parasites, and Disease

Brown (1975) and others have emphasized the importance of insects, parasites, and disease in modifying the structure of many western forests and, in turn, the frequency and intensity of subsequent fires. Relatively little quantitative work has been done on the effects of fire on plant diseases (Alexander and Hawksworth 1976, Parmeter 1977). Available evidence--particularly concerning fire and dwarf mistletoe (*Arceuthobium* spp.)--has been summarized by Alexander and Hawksworth (1975, 1976), Hardison (1976a, 1976b), Harvey and others (1976), Wicker and Leaphart (1976), and Parmeter (1977, 1978). The relationship between fire, insects, and forest structure has been discussed by Miller and Keen (1960) and Roe and Amman (1970).

In an overview of the impact of fire on pathogens, Parmeter (1977) concluded that, "Fire can alter disease activity in forests and scrublands directly by affecting the survival and development of pathogens or indirectly by affecting characteristics of plant communities, individual plants, or physical and microbial environments that influence pathogens." The relationship between fire and disease is complicated both by the variability of fire intensity and frequency and by the complexity of possible interactions between fire and disease.

In the absence of fire, numbers of trees infected, intensity of infection, and degree of damage increases with age of trees or stands and size of trees. The rate of spread through multistoried stands is also more rapid than through single-storied stands (Parmeter 1978).

Intense fires tend to have a sanitizing effect on infected stands giving lodgepole pine the edge over mistletoe, while partial burns create ideal conditions for rapid spread of mistletoe in even young stands (Alexander and Hawksworth 1976). Mistletoe, on the other hand, kills and stunts trees, causes spike tops and witches' brooms, which modify vertical structure of the forest, providing "ladders" for fire to ascend and consume tree crowns. This obviously increases fire hazard, flammability, and fire intensity. Fire may encourage spread of the mistletoe parasite by conversion of nonsusceptible climax spruce-fir forests to mistletoe-susceptible nearly pure stands of lodgepole pine (Alexander and Hawksworth 1976). At the same time, fire may limit development of natural genetic resistance to mistletoe by continually preventing survival of any trees that may have become somewhat resistant (Roth 1974).

Prescribed burning in pine plantations in the South reduced pine mortality and total infection by *Heterobasidion annosum* (*Fomes annosus*) root rot (Froelich and others 1978). The impacts of fire on the fungus were greatest where the disease was most serious. Although confirming field studies need to be carried out in western forests, Parmeter and Uhrenholdt (1975) have found that spore germination or mycelial growth of several fungi, including *Fomes annosus*, was reduced by exposure to smoke. By contrast, *Trichoderma* spp., common fungal competitors of *Fomes annosus*, increased in soil after

burning (Froelich and others 1978) and germination of Trichoderma spores was increased when exposed to smoke (Parmeter and Uhrenholdt 1975).

Age structure of lodgepole pine forests relates very strongly to potential for attack by mountain pine beetle (Dendroctonus ponderosae Hopk.); beetles first attack larger (14-inch diameter or more) trees which have thick phloem and a better food supply (Roe and Amman 1970). In addition, high-elevation stands show less infestation by pine beetles and greater infection by dwarf mistletoe (Amman 1969). Beetle activity in the absence of fire in the Northern Rocky Mountains leads to replacement of lodgepole pine by Douglas-fir at lower elevations and by subalpine fir and spruce at higher elevations. In the presence of fire, seedling lodgepole pine come in.

As an example, the 1961 Sleeping Child Fire burned more than 25,000 acres of lodgepole pine in the Bitterroot National Forest of Montana which had previously been heavily damaged by mountain pine beetle between 1928 and 1932 (Roe and Amman 1970). Lodgepole pine seedlings became established on about 15,000 acres of the burned area; within 80 to 90 years, these newly established pine trees will simultaneously reach sizes attractive to beetles over sizable areas. Then a widespread infestation of beetles will lead to heavy fuels which in time will lead to intense burning which may be followed by another restocking of lodgepole pine seedlings which will start the sequence again. In areas where mistletoe infection is heavy, tree growth is reduced, thus reducing the likelihood of beetle infestation. However, in that instance, the previously described changes in vertical structure which mistletoe brings about also lead to fire hazards and burning.

In ponderosa pine forests, Miller and Keen (1960) found that western pine beetle (Dendroctonus brevicomis) populations concentrate in fire-injured trees which survive a fire. They noted that unburned stands of ponderosa pine had larger numbers of small trees than burned areas, but that burned areas had larger trees and larger volume per acre. Thus, they concluded that in general, "...the long-term effect of fire is to lessen western pine beetle damage rather than increase it."

It would appear that man's efforts to decrease fire frequency often lead to conditions favoring growth of forest insects or disease organisms. Such growth in turn affects forest structure and fuel buildup in a way which insures the forest will burn, sometimes with greater intensity than would have been the case otherwise.

Stability, Diversity, and Resilience

Bonnicksen and Stone (1978) note that in the absence of frequent fire in sequoia-mixed conifer forests, there is not a steady state mosaic. Instead, younger aggregations are being replaced by older ones. There is no fire to make new openings and no opportunity for seedling and sapling white fir to become the top tier dominant in such new aggregations. Keeley (this volume) has suggested that frequent fires are an important part of the fire regime, because they preserve seed trees by preventing widespread crown fires among species such as ponderosa pine which have no means of storing seed on trees or in the soil. Under a periodic fire regime in a mixed-conifer ecosystem, Agee and others (1978) point out that ecosystem dynamics appeared to be more stable. Low decomposition rates and the flammable nature of the forest floor in this system assured that frequent surface fires would occur, periodically releasing stored energy.

"If stability is defined as the ability to resist change, then...vegetative cycles maintained and driven by fire must be considered to be stable" (Vogl 1970). As such, lodgepole pine communities and other fire types would be considered very stable, because fires in such types result in a replacement community of similar structure to that originally found there, while fire in climax types results in extreme change (Brown 1975). On the other hand, when natural fires are suppressed in a mixed conifer forest, biomass and energy accumulate, species composition shifts, the new system is

less flammable, ladder fuels build up in understory trees, and a wildfire which does occur is much more likely to become a high-intensity crown fire, killing mature trees and seriously disrupting the system (Kilgore and Sando 1975, Agee and others 1978).

Loucks (1970) believed that community stability, species diversity, and annual productivity are positively related. He offered the hypothesis that "...evolution in ecosystems has brought about not only adaptation to heterogenous environments, but adaptation to a repeating pattern of changing environments, a stationary process that represents a composite of time intervals over which replacement of species is repeated over and over again." As a part of their study of fire-dependent forests in the Northern Rocky Mountains, Habeck and Mutch (1973) offered a similar hypothesis that, "...the diversity of community life forms engendered some sort of ecosystem equilibrium or a kind of biologic 'check and balances' system that governed the magnitude of the effects accompanying a given forest fire." Taking this a step further, one could also assume that simplifying the community life forms by eliminating fire may modify forest structure in a way that brings imbalance to the natural system. Taylor (1973) found that elimination of fires in lodgepole pine communities in Yellowstone National Park, Wyo., limited ecological diversity by reducing or eliminating those plants and animals found only in successional communities present before closure of the forest canopy.

A different point of view is found elsewhere in the ecological literature. "Resilience" has recently been defined as "the ability of a natural ecosystem to restore its structure following acute or chronic disturbance..." (Westman 1978). This set of properties was included under the term "stability" in earlier work by May (1973), Holling (1973), and Orians (1975). Westman (1978) suggests that "stability" be limited to the "pattern of fluctuations in a relatively unimpacted ecosystem over time" and cites work by Whittaker (1975) to support this. The ability of a system to resist displacement in structure and function when subjected to a disturbing force (such as fire) has been referred to as "inertia" by Orians (1975) and Westman (1978). Holling (1973) had termed this same property "resilience," while Vogl (1970) had called it "stability."

Botkin and Sobel (1975) have pointed out that "stability" in the anecdotal literature has often been implicit and vague. Where it was defined, the concept was similar to the "static stability" found in a classical mechanics system that returns to equilibrium after being disturbed. Such definitions are found in Odum (1971), Krebs (1972), and Smith (1974). Holling (1973) and Botkin and Sobel (1975) contend that such a static stability concept, borrowed from classical physics, may be inappropriate for the analysis of ecosystems in that, "Natural undisturbed systems are likely to be continually in a transient state" (Holling 1973).

Using the example from Heinselman's (1973) history of the 100-year return interval for fire in the forest of the Boundary Waters Canoe Area of Minnesota, Botkin and Sobel (1975) maintained that the concept of an equilibrium state for a natural forest has been contradicted by history and that static stability is a concept with little ecological value. They ask the question: "What does it mean to 'stabilize' or 'preserve' a forest when the natural undisturbed forest is changing through time, and when fire appears to be an intrinsic event?" They feel that the analysis of stability and its dependence on ecosystem complexity must be broadened to include "notions of stability besides the definition of static stability borrowed from statistical mechanics."

May (1973) contends that in the natural world, "it is not true that population stability is uniformly associated with trophic complexity and faunal and floral diversity." On the contrary, a number of natural monocultures, such as the march grass (*Spartina alterniflora*), are very stable; the instability of man-made monocultures results not from their simplicity, but from their unnaturalness. As a mathematical generality, May (1973) contends that increasing diversity and complexity enhance

community instability. But he also notes that we need much better understanding of principles which govern natural associations of plants and animals. This can be primarily gained by studies in pristine ecosystems such as those found in National Parks and Wildernesses.

CONCLUSIONS

Fire suppression has caused an increase in intervals between fires in many areas. This decrease in frequency is leading to an increase in surface fuels in many forests and a modification of forest structure.

This structural change is manifested as a shift in the distribution of ages and species composition in various forests and scrublands of the West. In turn, these changes in age classes and species composition affect both the horizontal pattern and vertical structure of the forest. Such structural changes lead to significant modification in the vertical and horizontal fuel arrangement of the forest--including an increase in ladder fuels--and hence to changes in probable intensity of future fires. In many cases, these changes appear to lead toward higher intensity fires in forests which previously had frequent, low-intensity fires as a normal fire regime. Changes are less noticeable so far where long return interval, high-intensity fire regimes are involved.

Such shifts in frequency of burning--which lead to changes in structure--also modify the intensity of subsequent fires, and in turn can lead to substantial changes in postfire forest structure. This new and different forest structure can in turn lead to changes in both frequency and intensity of subsequent fires.

The complexities of these interactions in any given forest are further compounded by (1) the very large number of possible species combinations in various geographic zones and (2) the variations which topography and weather can bring to the impact of a given frequency and intensity of fire on various vegetation types.

There is great need for additional knowledge about natural fire regimes--involving both frequency and intensity--in many forest types of the West. But there is also need to take full advantage of what we already know and to apply this knowledge in management of our forest and scrubland ecosystems. In summary, as has been pointed out elsewhere (Kilgore 1976), we need better understanding of fire as a process and as a tool, but we also need greater commitment by land managers to use on the land the best of what we already know. To carry out an effective resources management program in western forests and scrublands, we will also need a well-trained cadre of fire managers who understand fire behavior under a variety of vegetation and weather conditions. To be fully successful as scientists, laymen, and environmentally concerned citizens, we must also work to gain greater public understanding of and involvement in developing and approving our land management practices.

Just as the fire process is basic to the operation of many ecosystems in the West, so our understanding of fire regimes is basic to our management of such ecosystems in National Parks, Wilderness Areas, and other public lands. With firmer knowledge and insight into how fire frequency and intensity relate to the structure of these systems, we can begin to use fire as a tool to best simulate its natural role in these areas.

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GRASSLANDS AND FIRE

Clair L. Kucera

Professor of Biological Sciences
University of Missouri
Columbia, Mo.

ABSTRACT

Most grassland environments are conducive to the ignition and spread of fire. The vegetation provides flammable fuel which when burned facilitates new growth and restricts tree encroachment. The grassland community exhibits various adaptations to fire environment. Fire intensity and frequency of burning are important variables in effecting its stability. Higher frequencies are associated with the moist grasslands where the potential for fuel accumulation is greatest. Grazing reduces litter buildup promoting less frequent fires. Excessive utilization by herbivores results in extended intervals or even cessation promoting site deterioration, composition changes in the plant community, and tree invasion.

KEYWORDS: encroachment, flammability, frequency, fuel, stability

INTRODUCTION

Grasslands comprise a significant portion of the earth's plant cover. One-fourth or more of the total vegetation consists of primarily herbaceous communities in which the Gramineae are the dominant life form. In a comingling with other species, the grasses give character and unity of vegetal structure to the landscape. Under certain conditions an overstory of scattered trees and shrubs may be present, as in forest-prairie transitions and tropical savannas. The terms prairie, steppe, veld, pampas, and savanna, among others, are used in a specific context of geography, geology, climate, soils, and physiognomy for designating a grassland type. Tundras, classified as a separate Biome, might be considered arctic or alpine grasslands on the basis of floristic components. Grasses and grasslike plants are significant members of most tundra communities.

Grasslands in the broadest concept have a universal distribution. They occur from continent to continent through a wide range of latitude. The North American Biome, the most extensive of all continental grasslands, extends from Saskatchewan in western Canada to Mexico, and from the Colorado plains to the mid-Mississippi Valley. In addition there are extensive grasslands in the intermountain region, in California, and in the Pacific Northwest. Other important types are the Eurasian grasslands, the East African savanna, the llanos of northern South America, and the widespread and varied types of

southeast Asia. Continental grasslands as wide-ranging systems are usually situated in an intermediate position on the moisture gradient, between uniformly humid climates and those marked by low and uncertain rainfall. Parent materials, topography, geologic history, biotic influences such as herbivores, and fire are also controlling factors. Other grasslands or grasslike communities, more restricted or localized, such as the sawgrass type of the Everglades of south Florida may be especially affected, and owe their existence in a high-rainfall regime to a particular set of factors including fire. Grasslands are replete in their variety, causation, and distribution.

The grasslands have been an historical base for intensive use by man, and have been subject to modification since his earliest culture. Included in this association with grasslands and savannas around the world dating back tens of thousands of years is his role as game hunter, nomadic pastoralist, and agrarian. Today much of the more humid parts of the original grassland, especially in the temperate latitudes, has been depleted by an expanding agriculture. Semiarid and desert grasslands everywhere are often overgrazed. Evidence from palynology and archaeology suggests that fire was significant in maintaining as well as expanding grassland, ignited either by natural causes such as lightning, or by man, or both. Much remains to be learned about the grassland resource in all its forms, and the potential for ecologically sound management and conservation.

The purpose of this paper is to examine the role of fire as an ecological influence in the grassland environment. The question of its relative importance under varying climates will be discussed. Furthermore, what are modifying factors which either accentuate or diminish the functional aspect of fire in grassland stability? Several are suggested, including grazing pressure by large herbivores, the effect of human activities, and the numerous implications of drainage, soil-water regimes, and characteristics of terrain. Other questions may be posed dealing with frequency and intensity and the functional relationships to fuel accumulation, flammability, and ignition sources. Do patterns or regional trends occur, for example, in requisite frequency across the inherently wide range of grassland variation?

GRASSLAND HISTORY

In sedimentary deposits on the northern plains of the United States, the fossil record offers evidence of change from forest to grassland millions of years ago. Here is documented a pattern of change in diet and food habits of various herbivores, an evolution from browser to grazer. Climate was changing, becoming less humid with geologic upheaval. The western plains became a vast "rain shadow" of the Rocky Mountains. In one evolutionary line of the horse, fossilized bones and teeth show development from a small forest browser to its modern descendant as a grass consumer. Such evidence from paleontology attests to the occupancy of an ancient Tertiary grassland but offers little concerning the floristics and structure of the plant community. More may be learned from the Pleistocene record about implied shifts in plant taxa on the landscape. In temperate latitudes of the Northern Hemisphere with its large continental masses in both North America and Eurasia, climates were especially subject to fluctuation, manifest in the advance and retreat of glaciers. In the Southern Hemisphere the much larger sea-to-land ratio precluded the same degree of climatic fluctuation and continental glaciation.

In North America and Eurasia during the late Pleistocene, climatic changes are inferred from the fossil record as an ebb and flow of grassland and forest (Frenzel 1968, Wells 1970a). Tree pollen ranging in age from 10,000 to 20,000 years was recorded in grassland sites from the United States and Canada. No forest stands occur at present within a minimum distance of 160 kilometers. Many of the localities revealed spruce (*Picea*) pollen as the principal fossil, especially in the central and northern plains. In the south, oak (*Quercus*) and juniper (*Juniperus*) were dominant. The grasslands of the North American continent, then, assumed contemporary status in

relatively recent times, possibly within the last 10,000 years. Martin (1975) noted that these grasslands cannot be traced back in the fossil record past 11,000 years. The late Pleistocene record in South American vegetation is less clear. Pollen data are available from only a few localities. The presence of ephedra (Ephedra) in the pollen spectrum from the Argentine would indicate a cold, steppe-like climate in the "rain shadow" of the Andes (Hester 1966). The few studies which are available do suggest, however, climatic shifts, several of which are synchronous with those of late Wisconsin period in North America.

The floristic affinities and the implication of historical ties between grassland and forest in North America have been evaluated (Wells 1970b). Several well-known "grassland" genera are represented as synusial components in climax forest of the eastern United States. Furthermore, many of these genera, including bluestem (Andropogon) have more species in forested regions than in the grassland itself (table 1). Similarly, Ross (1970) showed the relationship of grasshoppers and lateline leafhoppers, both characteristic grassland groups, to surrounding biomes. In this study, 108 species of grasshoppers occurred in the grassland but only three were endemic. The same trends were shown for the leafhopper species, there being very few prairie endemics. Illustrated here are the close biological interactions between grassland and forest, most sensitive in tension zones but also possible between distant locales. The relative ease and facility of vegetational shifts initiated by climatic change is implied, mediated by other factors including fire and its use by primitive man. During xerothermic periods, fires probably assumed increasing importance in the eastward expansion of grasslands, and the opposite in pluvial times when forests advanced on the latter (Gleason 1922, Transeau 1935, Sears 1942).

Pleistocene glaciation as observed in North America and Eurasia had less impact on tropical vegetations. Temperature fluctuation at least to the degree experienced in higher latitudes probably did not occur. Because of generally less favorable conditions for fossilization and preservation in the low latitudes those changes in vegetation which did take place in the tropics are sparsely documented in the palynological record. However, the extinction or decimation of large segments of the grassland megafauna provides some clues of change (Guilday 1967). Fossils of zebra, antelope, and other grazing animals have been found in the Sahara. Some of these records are dated as recently as 4,000 years ago. Increasing desiccation was a primary factor. With drying conditions the grasslands retreated southward with their complement of surviving herbivores to present locales of extensive savanna in East Africa. Desiccation is also proposed for the extinction of numerous large herbivore species in the grasslands of Australia and South America within the last 10,000 to 20,000 years. In the long history of grasslands it is seen that marked changes in distribution patterns and species composition did occur in a relatively brief period of time. With the advent of man in the Pleistocene and his subsequent domination of nature with fire, vegetational change would be accelerated.

Anthropomorphic fires in maintaining and expanding grasslands and savannas are discussed by Stewart (1956) and Sauer (1975). The presence of charcoal deposits and various artifacts in ancient dwelling sites point to the human factor and the beginning of man's influence in grassland environments using fire. This influence is measured in several hundreds of thousands of years, first as "kept" fires borrowed from natural causes such as lightning and volcanism. Much later, within the last 30,000 to 40,000 years, man learned to make his own fires at which time his impact on vegetation through its intentional use would have been greatly enhanced. As the site of human antiquity, the tropics have been under the influence of man and his new-found tool for the longest duration. The evidence suggests that extensive areas of tropical savanna are the result of burning the forest edge and clearing such tracts for grass and agricultural plots (Stewart 1956, Batchelder and Hirt 1966, Hopkins 1968, Olindo 1971, Scott 1977).

TABLE 1.--Regional representation of important grassland genera in the Eastern Deciduous Forest Biome and the Central Plains^{1/}

Genus	"Prairie" spp. native in the Carolinas	Species in the Carolinas	Species in the Central Plains
- - - - Per genus - - - -			
<u>Andropogon</u>	<u>A. scoparius</u> Michx	7	4
	<u>A. Gerardi</u> Vitm.		
<u>Panicum</u>	<u>P. virgatum</u> L.	62	6
<u>Sporobolus</u>	<u>S. heterolepis</u> Gray	7	7
<u>Crotolaria</u>	<u>C. sagittalis</u> L.	6	1
<u>Lespedeza</u>	<u>L. capitata</u> Michx	10	3
<u>Psoralea</u>	(none)	5	14
<u>Artemisia</u>	<u>A. caudata</u> Michx.	1	15
<u>Aster</u>	<u>A. oblongifolius</u> Nutt.	40	14
	<u>A. patens</u> Ait.		
<u>Coreopsis</u>	<u>C. lanceolata</u> L.	11	5
<u>Kuhnia</u>	<u>K. eupatorioides</u> L.	1	1

^{1/} Adapted from Wells, P.V. 1970. Historical factors controlling vegetational patterns and floristic distributions in the Central Plains of North America. In Pleistocene and recent environments of the Central Great Plains. Dort Wakefield and J. Knox Jones, Jr., eds. p. 211-221. Spec. Publ. 3. The Univ. Press of Kansas, Lawrence.

THE GRASS-FIRE ENVIRONMENT

Dried grasses and suitable meteorological conditions at least during certain times of the year are a partial basis for a grass fire environment (Daubenmire 1968, Wells 1970b). Furthermore, grassland terrain is characterized by generally unbroken upland, free of advanced dissection, and relatively distant from water sources such as streams. Under conditions of topography, combustible materials, and low humidities coupled often with high winds, the ignition and flammability would be accentuated in grasslands. Predictions of combustibility, flame dimensions, and rate of spread have been tested in prescribed burns using fire models (Sneeuwjagt and Frandsen 1977). It was found that useful predictions of grass fire behavior can be made; however, wildfires were not observed. Such models in future, however, may be useful tools in fire management of grasslands, in determining the most suitable time to burn.

A general difference in fuel conditions between grassland and forest is the ready ignitions of fuels in the former following even a brief dry period. The easily dried foliage presents a more or less homogeneous, somewhat diffuse, but contiguous fuel source for sustained ignition. Such fires also generate less extreme temperatures than those in forest which, once ignited, provide a hotter fire with generally greater fuel supply. Thus, forest fires are generally more destructive to the site and to plant life itself. Soil nitrogen and organic matter are volatilized and erosion is accelerated. In understanding the fire effect in the ecosystem, the intensity factor as a function of fuel density and caloric content must be considered.

Komarek (1965) notes that lightning is a basic complement of climate in grasslands. Characteristic drought periods provide a mass of combustible fuel in conjunction with belated thunderstorm activity causing numerous lightning strikes but often very little precipitation. In a study of naturally occurring fires in Saskatchewan, Rowe (1967) concluded that lightning is a common cause of wildfires, and that the frequency of this combination event was 1 year in 6. In Kansas tallgrass, the incidence is higher ranging from two to five for a given 10-year period (Hulbert 1973). In tropical savannas, lightning-based fires are observed occasionally but are generally uncommon (Phillips 1965, Talbot and Kesel 1975). According to the latter authors, there is little evidence to support the contention that lightning is important as a source of ignition in tropical savannas. These authors note that lightning in the tropics occurs at the start of the rainy season when there is little fuel and the vegetation is wet. It is estimated that less than 2 percent of tropical fires are caused by lightning (Batchelder and Hirt 1966). Other reports would indicate, however, that more lightning fires in the tropics occur toward the end of long dry periods when the vegetation is in a dried state (Komarek 1971).

According to Wien (1976) the frequency of tundra fires is relatively low in comparison to the lower latitudes, and until recently, with increasing human activity, most fires were probably of lightning origin. Although not common such fires may be extensive (Buckley 1967). In the 19th century considerable alteration of caribou habitat occurred as a result of fire with subsequent expansion in range of moose. Tentatively, it would appear that lightning-caused fires are more frequent in the mid-latitude grasslands. Here a combination of fuel and weather provides suitable conditions for lightning ignition. At the latitudinal extremes, in tundra grasslands and in tropical savannas the sum effect may be lessened by deficiencies in one or both of these variables. Regardless of frequency or extent, lightning-caused fires are an integral part of the grassland environment (Vogl 1969).

Some grasslands are regarded as a natural climax, a stable, self-perpetuating stage in ecological succession. In these the controlling effects of fire are probably minimal. These permanent grasslands occur usually, but not always, under semiarid to arid conditions. Plant productivity is obviously lower than in more humid regions.

The vegetation produces less litter biomass, therefore, less fuel for sustained combustion. Furthermore, the longer equilibrium time required to reach maximum litter accumulation means that frequency of naturally occurring fires is lessened compared to more rapid accumulation in tallgrass communities. In general, those grasslands with diminished productivity potential for reasons of moisture deficiencies or cold or both are less fire-dependent than their counterparts in more humid regions.

Vesey-Fitzgerald (1971) in discussing the impact of fire and grazing in the Serengeti ecosystem states that fire plays no part in the development and stability of the treeless, semiarid shortgrass plains. A climatic and edaphic equilibrium has been achieved. Shortgrass vegetation of the western Great Plains in the United States is a comparable temperate zone example. Borchert (1950) and Weaver and Albertson (1956) considered the North American grassland as a whole a climax vegetation controlled essentially by climate, even though fire may be present. Similar views are shared by Eden (1974) and van der Hammen (1974) for the origin of Central and South American savannas. The whole question of the role of fire in natural grasslands in certain locales still is a matter of debate, both as to their origin and maintenance (Vogl 1974). It may be concluded, however, that fire is but one of several factors made more effective in an environment conducive to the establishment and stability of the grassland community.

In the New World tropics, extensive savanna vegetation occurs on old landforms or peneplains with fluctuating water regimes, ill-drained soils, and low nutrient content. Here edaphic factors are considered primary ecological controls of savanna stability, although these grasslands are periodically swept by fire (Beard 1958). The recurrence of fire would suggest its implications in savanna maintenance, particularly in view of the high rainfall received in most neotropical savannas (Sarmiento and Monasterio 1975). Long dry seasons do occur, however. Savannas of the Old World characteristically occur in lower rainfall regimes, particularly those of Africa.

Some grasslands and savannas are acknowledged to be fire dependent. These are quasi-climaxes maintained so long as fire is part of the environment. They represent secondary or derived stages of the succession (Vesey-Fitzgerald 1971). The succession is arrested in a seral stage dominated by grasses and other herbaceous species, or shows deflection from potential climax by long and continuous disruption through fire. If fire ceases, the entry of woodland species is most commonly observed, many of which are fire tolerant or fire adapted (Vogl 1974). The potential for woody invasion is greater in these fire-dependent grasslands than in climatic or edaphic grasslands. In various types of savanna and veld in Africa, frequent fire is an important factor in control of brush and grassland improvement (Brynard 1971, Pratt and Knight 1971, Strang 1974). Most probably, it is in secondary and derived grasslands that fire has the most significance as an ecological control.

The tropical savannas are the most extensive of the world's grasslands (Budowski 1964). Fire is a common occurrence in this grassland type (Sarmiento and Monasterio 1975). This is primarily due to the use of savannas for forage by domestic animals. In the Serengeti savanna, Masai herdsman are responsible for most fires. The main period for fires is in the latter part of the dry season or during short rainless periods (Vesey-Fitzgerald 1971). It is difficult to find savanna areas which have escaped burning for long periods. Most are burned every 1 to 2 years. While certain savannas probably are maintained by periodic fires in conjunction with controlling influences such as poorly drained soils, many others are thought to have an anthropogenic origin (Blydenstein 1967, Lemon 1968, Scott 1977). Human activity, once initiated, maintains and expands the savanna at an accelerating rate through the use of fire. As savannization continues and natural woodlands diminish, it is thought that continued use of fire in the tropics effects relatively long-term shifts in vegetational equilibrium.

SELECTION EFFECTS

The long and continuous presence of fire in some grasslands is a selection factor in developing fire-resistant and fire-avoiding strategies and adaptations in plants. Grassland species exhibit a number of characteristics suited to the fire-susceptible environment, where desiccating winds, low humidities, and generally low soil moisture are commonplace. Fire-dependent communities are hypothesized to burn more readily than non-fire-dependent ones because selection has favored traits which make them more flammable (Mutch 1971).

Annual growth dies back each year to become a combustible source of fuel, with no harm generally to underground systems. With some exceptions, a majority of grassland species are perennials with relatively large functional biomass belowground. Studies show that soil temperatures 1 inch (2.5 cm) below the surface rise very little in the active fire zone (Scotter 1970). At 3 to 4 centimeters there is no rise at all. Thus, fire consumes only aboveground biomass which generally is nonfunctional in a cured state at the time conditions are most conducive for burning. In addition, the amount of biomass available in grass communities does not provide the high air temperatures typical of forest fires, and the fire does not typically burn into the grass crown or base (Humphrey 1974). Even when green shoots are destroyed, resurgence in growth after the fire is possible from protected organs in the soil. These include rhizomes, bulbs, corms, and basal meristems, although these, too, may be destroyed in some species. Wright (1974) noted the killing back of sideoats grama (Bouteloua curtipendula) following fire in both wet and dry years. In this species the rhizomes were damaged. Other species were not similarly affected, however, showing a differential response of the grassland species themselves to fire.

The grasses, other monocotyledons, and many herbaceous dicotyledonous species have a selective advantage over ligniphytes with characteristically aerial growing points. The grassland life-form spectrum based on Raunkaier's classification shows a high percentage of the plants which are hemicryptophytes and geophytes. Various phanerophytic types also are represented. Most of these woody invaders, many typical of the grassland habitat or transition zone, sprout readily when stems are killed by fire. In prairies of the Middle West, Ulmus, Quercus, Populus, and many members of the Rosaceae are prolific sprouters. Generally, with more severe destruction of the aerial portions, sprouting becomes visibly more prolific at the base. Humphrey (1974) lists several sprouting trees and shrubs in desert grasslands, including species of Chrysothamnus, Prosopis, Purshia, and Tetradymia. Another woody invader, Haplopappus, may sprout prolifically if burned in the flush of new growth. Otherwise, it is typically a nonsprouter. In Uganda 30 to 40 species of trees characteristically sprout after burning the tallgrass savanna in which Hyparrhenia is a dominant grass (Bueckner and Dawkins 1961). The season of year in which the burn occurs has a marked effect on the degree of sprouting (Brynard 1971). In the South African veld where Hyparrhenia also was dominant, tree sprouting was more abundant after spring burns than at any other time.

Fire may favor sexual reproduction in some nongrass species, through dehiscence and dispersal of seed. For the herbaceous layer of the "campo cerrado" in Brazil Coutinho (1977) showed that dispersal by wind was increased from fruits opened by fire. The success of these species indicated a fire dependency. In California annual grassland, grass seed deposited on the ground or in the surface soil survive fire (Hervey 1950). Fire does not significantly alter seed production in the annual type (Heady 1972). Fire-stimulated annuals are seldom jeopardized by fire before seeds are produced because of generally low fuel supply. According to Vogl (1974) conditions for seed germination and early growth often are enhanced by fire.

Both grazing and fire select for species which are capable of regenerating from ground level or below, but not necessarily the same species (Lloyd 1968). Such a system provides for diversity as well as survival value. Handley (1969) discusses the evolution of grasslands and wild grazing mammals as an intricate relationship involving a long history of natural fire. In southeast Asia, wild cattle (Bibos sondaicus) exhibit a distributional dependence on man-induced fires (Wharton 1968). The ecological effects of fire in grassland are inseparably related to grazing (Hill 1971). Fire's is lessened under conditions of overgrazing. Fire frequency decreases as the fuel potential is reduced and the vegetational shifts to woodland species often occur. The trend applies to both tropical and temperate grasslands, with fire becoming less frequent under heavy grazing (Humphrey 1963, Pratt 1967, Vesey-Fitzgerald 1971). Hervey (1950) noted that heavy grazing reduced grass cover in a California annual grassland 50 percent compared to light grazing. Under the latter conditions the effects of fire were less evident. During periods of drought, which also cause site deterioration and loss of cover, fires have less influence on compositional changes than wet years (van Wyk 1971, Wright 1974). Herbivores and fire provide an historic combination suited to the stability of the grassland system. There are no natural or climax grasslands without an herbivore fauna according to Martin (1975) who advocates the use of browsers and grazers in restoring the grassland equilibrium.

VEGETATIONAL CHANGES

Fire in vegetation has been widely observed and reported in the scientific literature since the early development of plant ecology as a discipline. Yet, the intrinsic role of fire in succession of plant species and its effect on structure of vegetation perhaps had been initially overlooked (Vogl 1974). In succession, fire serves as a retrogressive agent as well as a stabilizing one. In transition zones between forests and grasslands the dual effect is perhaps most enhanced. The occurrence as well as discontinuance of fire provides a basis for analyzing and interpreting its significance as an ecological factor in vegetative cycles.

Fire in North America was a part of the presettlement environment. An early report in the science literature (Wells 1817) documents the widespread nature of fire in the prairies. The frontier chronicles also publicized the occurrence of spectacular fires throughout the grassland region (Jackson 1965). These wildfires which burned uncontrolled were often set by the Indian. This practice is similar to the use of fire by African peoples in maintaining open grassland conditions. In appraising the history of fire, one can readily appreciate the impact of man and his acquisition of fire in reshaping vegetation. Cessation of fire, combined with intensive land use following settlement, also has far-reaching results. In the North American grassland, the invasion of woody species into grassland has occurred in the Midwest to the high plains and into the southwestern grasslands. Community structure is being altered with concomitant changes in forage production and nutrient processes. The gradual shift from a grazing potential to the increasing browse resource is widespread.

Forest Interactions

Numerous studies document the significance of fire in maintaining a grassland equilibrium. For Kansas tallgrass prairie (Bragg and Hulbert 1976) a 34 percent increase in wood plants occurred on plots unburned for 32 years. Important invaders included Ulmus, Juniperus, Quercus, Rhus, and Symphoricarpos. On periodically burned sites, wood cover was held to presettlement densities based on section-line data. In western Minnesota, prairie openings protected from fire are disappearing with encroachment by aspen (Populus tremuloides) (Svedarsky and Buckley 1975). A vegetational analysis based on witness tree records of the original land surveyors indicates that oak openings have given way to dense forest in southwestern Wisconsin (Cottam 1949). The reason given for increasing forest densities is the cessation of Indian fires over the last century. American elm (Ulmus americana) was a rapid invader on a wide front

in unburned prairie in Missouri (Kucera 1959). Heavy-seeded oaks (Quercus spp.) were limited to a narrow band at the prairie edge. Eastern redcedar (Juniperus virginiana) was sporadically distributed in control areas. None occurred in recent burns. It is one of the most fire-sensitive species and like most conifers does not produce sprouts. In the Oklahoma prairie-woodland transition wildfire was also effective in killing eastern redcedar. The two principal oak species, post oak (Quercus stellata) and blackjack oak (Q. marilandica) were killed back but survived by sprouting (Penfound 1968). Growth of new grass was later heavily used by bison supporting the widely held view that burned grasslands around the world are preferred by herbivores (Anderson 1965, Pratt 1967, Eltringham 1976).

In the southwestern grasslands of the United States extensive tracts have been adversely affected by invasion of mesquite (Prosopis). Overgrazing is a contributory cause. Site deterioration and loss of plant cover caused by excessive animal pressure combine to lower forage production, fuel accumulation, and the incidence of fire, whether by man or other sources. Many areas were essentially brush free 50 years ago (Humphrey 1963). Other studies in the semiarid grasslands also point to periodic fires as an integral part of presettlement environment. Cable (1965) noted that mesquite mortality was highest following fire, spring burning being the most effective time to control this species when invading grassland (Sharrow and Wright 1977). The resurgence of juniper (Juniperus scopularum) was attributed to fire cessation in Idaho grasslands (Burkhardt and Tisdale 1976). In the prairies of western Canada, fire is considered an important historic factor in stabilizing the advance of widespread aspen woodlands from the north (Moss 1952). Halliday and Brown (1943) recorded aspen encroachment in the Canadian grasslands, the explanation being the cessation of fire since settlement and expanding cultivation. Similarly, tree invasion in the northern Great Plains of the Dakotas, Wyoming, and Montana is widespread where fires have been eliminated (Coupland 1961, Phillips and Shantz 1963). From these selected papers it is concluded that even in the drier sections of the American grassland periodic fire is necessary to offset tree and shrub invasion.

Similar results of bush and tree invasion are reported elsewhere in grassland habitats. In the African tall veld, long-range studies show extensive encroachment. During 15 years of fire control there was a 30 percent increase in tree density (van Wyk 1971). In drier regions of the African savanna, as in the American grassland, tree invasion occurs in the absence of fire (Skovlin 1971). Other reports attest to the significance of the fire factor in stabilizing the grass-tree interaction in the tropical savanna (Cook 1965, Phillips 1965, Pratt 1967, Pratt and Knight 1971, Daubenmire 1972, Strang 1974).

Fire thus retards tree invasion of existing grasslands, the frequency of which is dependent on a number of factors including rainfall (van Wyk 1971, Talbot and Kesel 1975). In regions of decreased moisture the recovery time for litter accumulation and successional change is prolonged, thus necessitating fewer fires than in humid regions to maintain the vegetational equilibrium. Repeated burning also decimates current forests and woodlands. In the vacated niches fire-adapted elements of the grassland become established. Increased light for the more xerophytic and shade intolerant grasses and herbs is a significant alteration of the original forest habitat. The fire process results in parklike grasslands and savannas and, if continued intensively, may lead to open communities dominated by grass (Strang 1974). The parklike grasslands and savannas usually consist of drought-tolerant and fire-resistant woody species with an understory of grass. The presence of scrub trees such as Brachystegia, Combretum, and Commiphora in African savanna is widespread (Phillips 1965). Trees are commonly short, with scrubby form. Studying an 80 km transect in Serengeti National Park which is frequently burned, Glover (1965) found that 71 percent of the trees were less than 1 meter tall. Many had enlarged rootstocks showing multiple fire scars. In the Rhodesian high veld, Strang (1974) reported that 30 years

of regular burning did not eliminate Brachystegia woodlands, although trees were stunted with frequent sprouting from the base. The fire-adapted grass, Themeda, among others, is an important species. Both life forms, grass and trees, are selected for and attuned to an environment in which repeated fire is a prime influence.

From these reports on the grass-tree interactions under a wide range of climatic conditions and fuel potential, it is feasible to draw several inferences on the relative significance of fire. If, under natural conditions, the grasslands were only moderately grazed by mobile herds of native herbivores, then a viable and competitive grass cover could better resist invasion by woody species. This, coupled with wildfire timed to cyclic accumulation of fuel, was probably sufficient to maintain a relatively open condition. In dry climates where fuel production is normally low, the interval between fires, of necessity, would be extended but adequate to arrest tree invasion since successional processes are characteristically slow. The burning potential in wetter climates would be synchronized to more rapid fuel accumulation, and therefore to shorter intervals between fires on a given site. Such fires would also have a greater intensity or caloric output per unit area.

Grass and Herbs Responses

Some species of herbaceous strata are benefited by fire, while others may be adversely affected. Still other species are checked by varying levels of mortality. The differential responses of grasses and broadleaved species to fire are a function of inherent tolerances as well as external variables including season of burn, moisture conditions, fuel supply, and subsequent growing conditions.

Cable (1965) showed that in dry years burning was destructive to certain grasses. A combination of fire and drought reduced little bluestem (Andropogon scoparius=Schizachyrium scoparium) as much as 42 percent (Wright 1974). In this study in West Texas, sideoats grama (Bouteloua curtipendula) was always damaged by fire. Little bluestem was also adversely affected in Oklahoma prairie (Penfound 1968), but in the same fire big bluestem (A. gerardi) increased in abundance. Various studies tend to show that this tall prairie grass is generally benefited by burning (Curtis and Partch 1950, Robacker and Miller 1955, Hadley and Kiekhefer 1963, Kucera and Koelling 1964). This coarse species with heavy rhizomes apparently is well adapted to fire. In Missouri a 60 percent increase in rhizome biomass was recorded for this species after 10 consecutive years of burning (Kucera and Dahlman 1968). While this distinction between fire plots and controls is amplified by the decline of big bluestem cover on the latter, fire nonetheless has a stimulating effect on growth and the competitive vigor of the species. In a study of fire in a western grassland, rhizomatous species were not harmed as much as those grasses with root crown at the soil surface (Conrad and Poulton 1966). Furthermore, moderate grazing tended to offset the deleterious effects of fire under those conditions. In general, it is seen that fire is more often harmful to the site in arid regions than in more humid ones, as measured in greater evaporation stress and accelerated erosion when litter is removed.

The selectivity of fire in grass composition is repeatedly shown in African grasslands. Frequent burning across a wide range of habitats from the veld to acacia savanna in East Africa results in conspicuous dominance of some species while others are decreased by fire. The red oatgrass (Themeda triandra) is favored by frequent burning so that under some conditions it is the dominant species (Pratt 1967, Eltringham 1976). Repeated burning also results in the selection of Hyparrhenia-dominated stands in some localities (Strang 1974). In Costa Rican savanna the introduced H. rufa was the only grass of African origin to benefit from annual burning (Daubenmire 1972). The effect of fire is shown in grass-forb relationships. Fire favors grasses over broadleaved herbs in some cases and not in others. When classed as groups and measured in terms of density or biomass, the former is generally increased. After 20 years of annual fire in Missouri, prairie grass species remained dominant while

nongrass species declined (Kucera and Koelling 1964). Data are summarized in table 2. Other studies may be cited in which fire supports grass dominance (Kelting 1957, Cook 1965, Wright 1972), but the specific causes in this fire relationship between grasses and nongrasses of the plant community remain unclear.

The biological tolerances and ecological factors involved in their many combinations affect community composition and structure, but by their complexity deter an easy solution. The aggressive nature of coarse grasses especially in a burning regime gives the impression of an exclusive advantage. Yet there are numerous dicotyledonous herbs in the grassland which express fire adaptation, but exercise no exceptional dominance within the community (Lemon 1967).

TABLE 2.--Composition changes in Missouri prairie after 20 years of fire treatment

Taxa	Control plots		Annual burn		5-year interval	
	F ^{1/}	C ^{2/}	F	C	F	C
<u>Andropogon</u> spp.	100	11	100	28	100	13
Other grasses and grasslike spp.	17	1	20	5	20	2
<u>Solidago</u> spp.	30	C ³	17	A	30	B
Other broad-leaved herbs	13	B	7	A	13	B

^{1/} Frequency, percent, after Raunkaier.

^{2/} Basal cover estimates, percent quadrat area.

^{3/} Letter classes of increasing stem density, A < B < C.

FUNCTIONAL EFFECTS

Many studies show an increase in dry matter production following fire, others a decrease. This effect, in either enhancement or reduction, may be observed for several seasons after a single burn, but diminishes as litter builds up to prefire levels. Among the reasons for enhanced growth are factors associated with removal of litter, increased light for emerging shoots, warming soil temperatures following spring burning, and a more favorable C/N balance through accelerated decomposition and greater nutrient availability. Studies in Oklahoma prairie (Rice and Parenti 1978) show that higher soil temperatures during the first 3 months of the growing season were mainly the reason for increased productivity following spring burning. In general it may be concluded that productivity responses are more positive in the humid grasslands, as in the prairie region of the Middle West. Productivity increases ranging up to 100 percent or even more following spring burning have been reported for these tallgrass communities (Hadley and Kiekhefer 1963, Penfound 1964, Vogl 1965, Kucera and Others 1967, Hulbert 1969, Zedler and Loucks 1967, Hill and Platt 1975, Peet and others

1975). A significant part of yield increases from other studies is due to the greater number of flower stalks which occur on burned plots (Curtis and Partch 1950, Ehrenreich and Aikman 1957, Lemon 1968). Daubenmire (1968), summarizing work in Africa saw that burning increases production in relatively moist regions but was detrimental in the more arid sections of the savanna.

Reports of negative response (less growth when compared to unburned grassland) generally come from regions of less rainfall (Larsen and Whitman 1942, Dix 1960, Launbaugh 1964, Hadley 1970, Redmann 1978). In these areas characterized by short grasses and less ground cover, soil moisture is a critical factor. The removal of litter by fire should affect adversely infiltration and storage, and at the same time enhance evaporation losses from barren surfaces. Thus, the advantages of fire as it relates to grass production in humid prairies are outweighed by other factors including seasonal availability of water for plant growth. Data bearing on these differential responses to fire are summarized in table 3. The summer rainfall line which divides these two groups on a geographical basis is approximately 275 to 300 mm. In regions of less rainfall the buildup of litter following fire favors increased production through conservation of moisture. Where moisture is characteristically more plentiful, litter buildup between fires is a causal factor in reduction of growth. A simplified diagram illustrates this hypothetical relationship (fig. 1). The area where the curves overlap represents a transition where the same fire frequency is critical for both. In humid grasslands the greater litter accumulation offers more opportunity for ignition at more frequent intervals with yield sustained at a high level. In dry grasslands, slower accumulation expands the fire interval effecting a maximized production within the environmental potential.

A comprehensive view of fire in grasslands shows that the relationship between fire and productivity as a function of rainfall is probably not a simple generalization (Daubenmire 1968). Exceptions are cited, a principal case being increased production in intermountain grasslands of western North America. Since fire eliminated the Artemisia, which is sensitive to burning, it might be expected that the factor responsible for more growth of grass was less competition. This was not the case, however, as reentry of sagebrush was too slow to modify reduction of grass when fire was eliminated. Additional analysis of these relationships is required.

Variations in upland and lowland prairie responses to a common fire have been reported (Zedler and Loucks 1969, Hadley 1970). These discrepancies are attributed to differences in species in the physiographic gradient, as well as to phenological development. Cool season species such as bluegrass (Poa) are adversely affected by early fire whereas later-developing, warm-season species including bluestem (Andropogon) are given an advantage (Robacker and Miller 1955). Time of burning and/or differences in phenological development were also important factors in evaluating responses to fire (Penfound and Kelting 1950, Smith 1960, Anderson 1965, Vogl 1965, Owensby and Anderson 1967, Wright 1969). In general, the later the burn in spring just prior to emergence of green shoots, the greater the production of warm-season species in the tallgrass prairie. If burning is too early, lower production may result because of increased evaporation of soil moisture in the interval between fire and resumption of new growth. This may explain the decrease in production due to fire in the Flint Hills of Kansas (Anderson 1965, Owensby and Anderson 1967). In these studies, extending over 30 years, winter burns invariably resulted in less production than late spring burns. Since the northern prairies have proportionately more cool-season representation, spring fires may decrease production. In contrast, southern grasslands with a greater complement of warm-season species would tend to benefit by fire where moisture was ample (Hill and Platt 1975).

TABLE 3.--Effects of burning on grassland productivity from North American stations

Region	Control	Fire	References
	- - - - - <u>Plots</u> - - - - -		
Illinois	3,020	13,210 ^{1/}	Hadley and Keikhefer 1963
	3,610	5,910 ^{2/}	
Missouri	5,090	9,330 ^{1/}	Kucera and others 1967
	4,820	5,220 ^{2/}	
Iowa	3,490	7,500	Ehrenreich and Aikman 1957
Eastern Kansas	1,860	3,400	Hulbert 1969
Western Kansas	3,800	1,710	Launbaugh 1964
Wisconsin			
lowland	-	+ ^{3/}	Zedler and Loucks 1969
upland	+	-	
Western South Dakota	+	-	Larsen and Whitman 1942
Eastern North Dakota			
lowland	+	-	Hadley 1970
upland	-	+	
Eastern North Dakota	-	+	Dix and Smeins 1968
Western North Dakota	+	-	Dix 1960
Saskatchewan	+	-	Redmann 1978

^{1/}, ^{2/} Represent wet years and dry years respectively; all values expressed in $\text{kg/ha}^{-1}/\text{yr}^{-1}$.

^{3/} +, - = greater or less productivity on an annual basis.

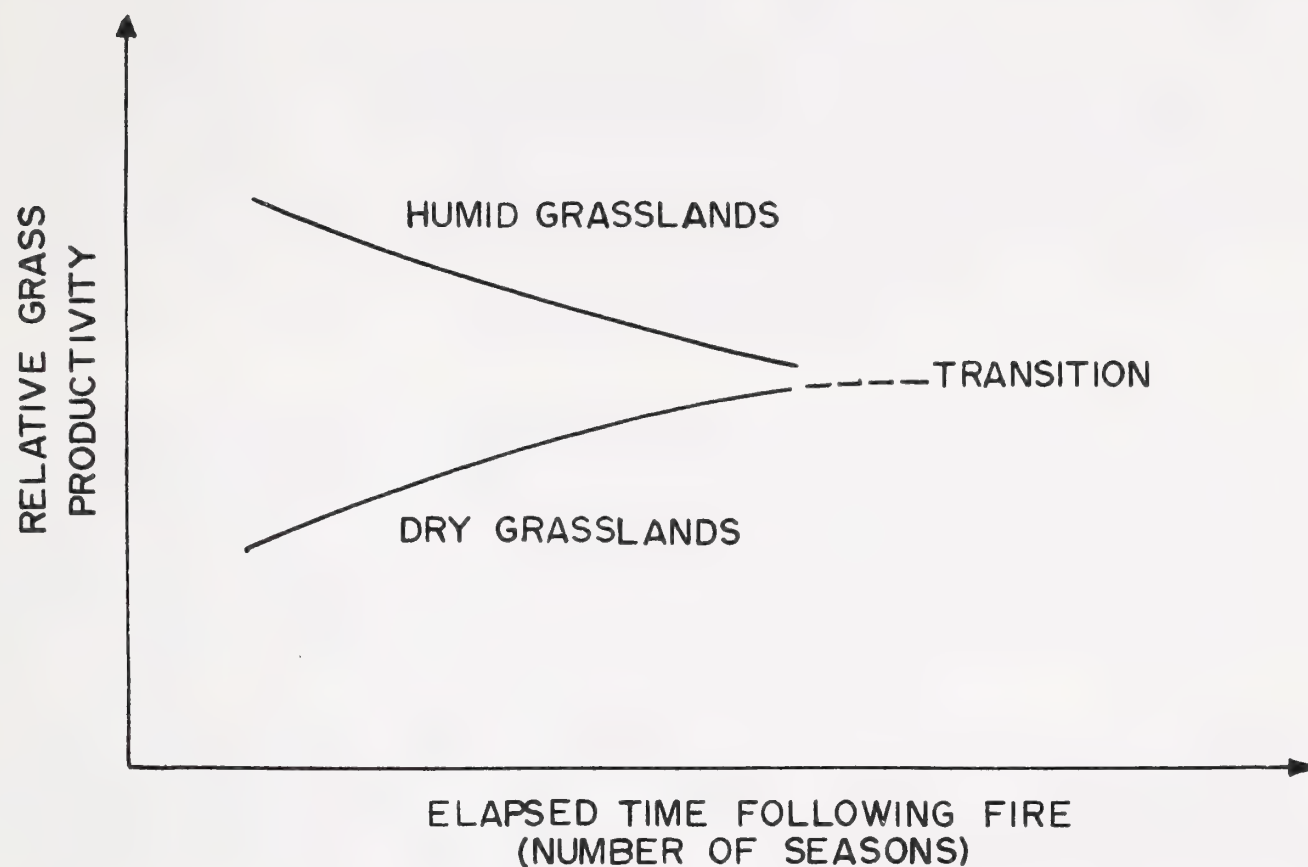


Figure 1.--Hypothetical relationship between grass productivity and fire frequency in different moisture regimes.

The magnitude of change in productivity evoked by fire is also modified by rainfall amounts from year to year. In unusually wet years the decrease in production associated with fire in typically dry climates is mitigated, and some increases may be noted (Wright 1974). Increases characteristic of humid climates are often much reduced in drought years. In Illinois and Missouri prairie similar trends were noted as drought common to both was accentuated (Hadley and Kiekhefer 1963, Kucera and others 1967). These comparisons are shown in table 3. Such trends suggest the changing impact of fire on a sliding scale of moisture availability on a year-to-year basis.

The effects of grassland fires are interwoven with the general climate as well as year-to-year variations in weather. This interplay of numerous biological and physical factors is involved in evoking a given fire response. In analyzing the role of fire in grassland function, long term observations are critical. This would enable the fire ecologist to appraise the gamut of effects, and thus better interpret the fire factor in developing a synthesis for all possible ecological conditions. Of particular importance is the seasonal timing and frequency of fire.

TIMING AND FREQUENCY - AN ASSESSMENT

The advantages and disadvantages of fire have been widely discussed (Humphrey 1963, Cable 1965, van Wyk and Wager 1968, Brynard 1971, Olindo 1971). Daubenmire (1968) and Vogl (1974) provide comprehensive reviews. The main advantages are removal of litter for improving growth conditions, increased palatability, greater abundance of forage particularly where moisture is adequate, and control of forest encroachment.

Disadvantages include greater runoff, soil losses through wind and water erosion, retardation of reproduction in some plants and on occasion the destruction of animal life. The seasonal timing and frequency of fire are so critical that results may either be beneficial or detrimental depending on local conditions. Precise data which are directly comparable from study to study are difficult to acquire. The impact of fire is dependent on a multiplicity of factors, and as is known fire conditions can vary widely between years, as well as from site to site. Thus, references specifically addressed to fire frequency as a requisite of grassland stability under a wide range of climatic and edaphic conditions are few and fragmentary. Perhaps the most extensive documentation is from the African veld region where studies on fire management have been going on for more than one-half century (Phillips 1965).

In American prairies, fires generally occur in spring and late fall and winter. The numerous studies in Kansas grassland indicate differential responses under prescribed conditions (Anderson 1965). Winter burning is more deleterious than spring fires because of soil and water losses in the interim before new growth and a protective cover are produced. Other studies tend to support these findings (Penfound and Kelting 1957, Kelting 1957, Owensby and Anderson 1967). The timing is especially critical in the drier grasslands where weather conditions are hazardous to moisture accumulations, especially on thin soils (Reynolds and Bohning 1956). In general, spring burning effects the best results in most temperate grasslands particularly for survival and growth of warm-season grasses. Under tropical conditions the most benefits are derived just prior to the rainy season to minimize site deterioration, at the time when resumption of growth is imminent (Brynard 1971, van Wyk 1971). Delayed fires occurring beyond the initiation date are harmful to the vegetation (Smith 1960).

Requisite frequency of burning to maintain grasslands is dependently related to rates of biological recovery and litter accumulation. In mesic climates these processes are relatively rapid indicating the requirement for short intervals between fires. With increasing aridity or cold the necessary interval would be expanded.

In Wisconsin prairie Vogl (1965) advocated a 2-year interval for maximizing grass production. While production is not necessarily related to community diversity and stability (McNaughton 1968), it does assess a state of vigor and competitiveness to some degree. Other studies in the Midwest indicate a range of 1 to 3 years as an optimum (Hadley and Kiekhefer 1963, Kucera and Koelling 1964). The latter authors found that on plots burned only once in 5 years, productivity was reduced to that on control plots, suggesting that litter accumulation was being maximized toward the end of this interval between fires. Incipient invasion by woody plants had occurred during this period. On plots burned every second year, productivity was similar to annual burning, but more diversity of species occurred. On this basis a burning frequency of once in 3 years was recommended for Missouri prairie. For more arid grassland in Texas, Wright (1972) indicated a burning schedule every fourth to seventh year. In the shortgrass and mixed prairie of western Kansas burning may not be feasible, unless tree control is needed (Launchbaugh 1972). The low incidence of natural fires in tundra (Wein 1976) suggests that fuel and meteorological conditions are generally not conducive to burning.

Fire frequency is generally higher in tropical grasslands than in their more temperate counterparts. Long dry season and flammable fuels coupled with high human densities dictate annual burning in most grassland regions. On an ecological basis, however, fire interval may be longer. One fire in 3 years is adequate to maintain present savanna conditions in those areas of more than 650 mm annual rainfall (Talbot and Kessel 1975). In areas of less precipitation the frequency would be less. Brynard (1971) recommended fire every third year to control bush invasion on and minimize site deterioration. In Ruwenzori National Park, where uncontrolled fires are common, a 2- to 3-year cycle is probably typical of the fire regime (Eltringham 1976).

The question of fire frequency, then, must be weighed against several ecological conditions if the grass community is to be maintained. In arid grasslands, natural fires were probably infrequent. Under some conditions they may not have occurred at all. Yet, we have seen tree encroachment in several temperate and tropical situations where fire was excluded over extended periods of time. Overgrazing is clearly a factor, causing fuel depletion and lower incidence of fire. In humid grasslands fire is even more critical, to arrest woodland invasion and prevent excessive buildup of litter. In both types of grassland the solution to the frequency problem is closely tied to herbivore use. The object of any experimental program is to prescribe a fire plan which preserves both plant and soil resources.

SUMMARY AND CONCLUSIONS

Grassland communities are adapted to an environment conducive to fire. Climates with dry periods provide combustible conditions for burning the vegetation. The grass community produces flammable residues which when consumed are not self-destructive. The major portion of the functioning biomass is protected at or below the soil surface where fire temperatures are reduced. Man's use of fire expanded the grassland at the expense of forest in relatively recent times, developing fire-dependent communities of grass and trees. Many savanna grasslands throughout the tropics are anthropogenic in origin.

The season and frequency of burning are the major determinants in effecting a balanced, self-perpetuating grassland community. Indiscriminate fires cause site deterioration and destruction of the biotic resource. Cessation of burning, however, may result in excessive litter accumulation and decline in growth, especially in humid grasslands. Bush encroachment occurs in most moisture types when fires are terminated or too infrequent. Under moist conditions in the grassland, a higher fire frequency is required to effect a balanced system, than in more arid grasslands. The rate of litter accumulation is more rapid. There is a faster recovery time of the floristic components. In arid grasslands these processes are extended, allowing for lower requisite frequencies.

The question of how frequently to burn is also related to herbivore utilization. Some degree of use reduces the amount of litter and probably expands the interval between natural fires. With overgrazing, depleted fuel supplies and possible cessation of fires result in woody encroachment. Most grasslands are overgrazed contributing to the widespread problem of invasion by woodland elements. Fire becomes a secondary factor when the carrying capacity as a grazing resource continues to deteriorate.

In general, most benefits are derived from burning just prior to resumption of growth in spring or before the onset of the rainy season. Extended periods between these two events cause excessive soil and water losses through erosion and runoff.

We may conclude that timing and frequency of fire are based on an understanding of several ecosystem characteristics of each grassland situation. These include litter accumulation, herbivore capacity, and the rate of successional change under given climatic and edaphic conditions.

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FIRE REGIMES IN SOUTHEASTERN ECOSYSTEMS

Norman L. Christensen

Associate Professor of Botany
Duke University
Durham, N.C.

ABSTRACT

Fire has significantly influenced the evolution of ecosystems throughout the Southeast, but particularly in the Coastal Plain. Fire frequency is a consequence of the frequency of incendiary events, landscape continuity, a complex set of moisture conditions, and the rate of fuel production. Changes in fire frequency or intensity may change the above features of an ecosystem thus altering the frequency and intensity of future fires. Fire response varies according to the natural role of fire. In areas when fire occurrence is stochastic and fires are intense, fire response is similar to classical successional schemes. In areas of chronic low intensity fires, fire may play an integral role in ecosystem stability.

KEYWORDS: southeastern USA, succession, fire intensity, fire frequency

INTRODUCTION

Although the southeastern States considered here comprise less than 20 percent of total area, nearly 58 percent of all wildland fires between 1960 and 1970 in the United States occurred in this region. This does not include prescribed fires which are used more widely in the South than perhaps anywhere else in the world.

The Southeast is divisible into three physiographic regions as shown in figure 1. The rate of forest fire occurrence (as number of fires per million hectares per year) is lower in the Piedmont and Mountain provinces than in the Coastal Plain province. However, within each province there is considerable variation in fire frequency and intensity associated with vegetational patterns and patterns of urban development.

The primary goal of this paper is to document the past and present variations in fire frequency and intensity within and between physiographic provinces in the Southeast. It is not possible here to discuss the role of fire in each ecosystem type found in the Southeast. Such general reviews can be found in Wells (1942), Garren (1943), and Komarek (1974). Rather, I have selected ecosystems for discussion which

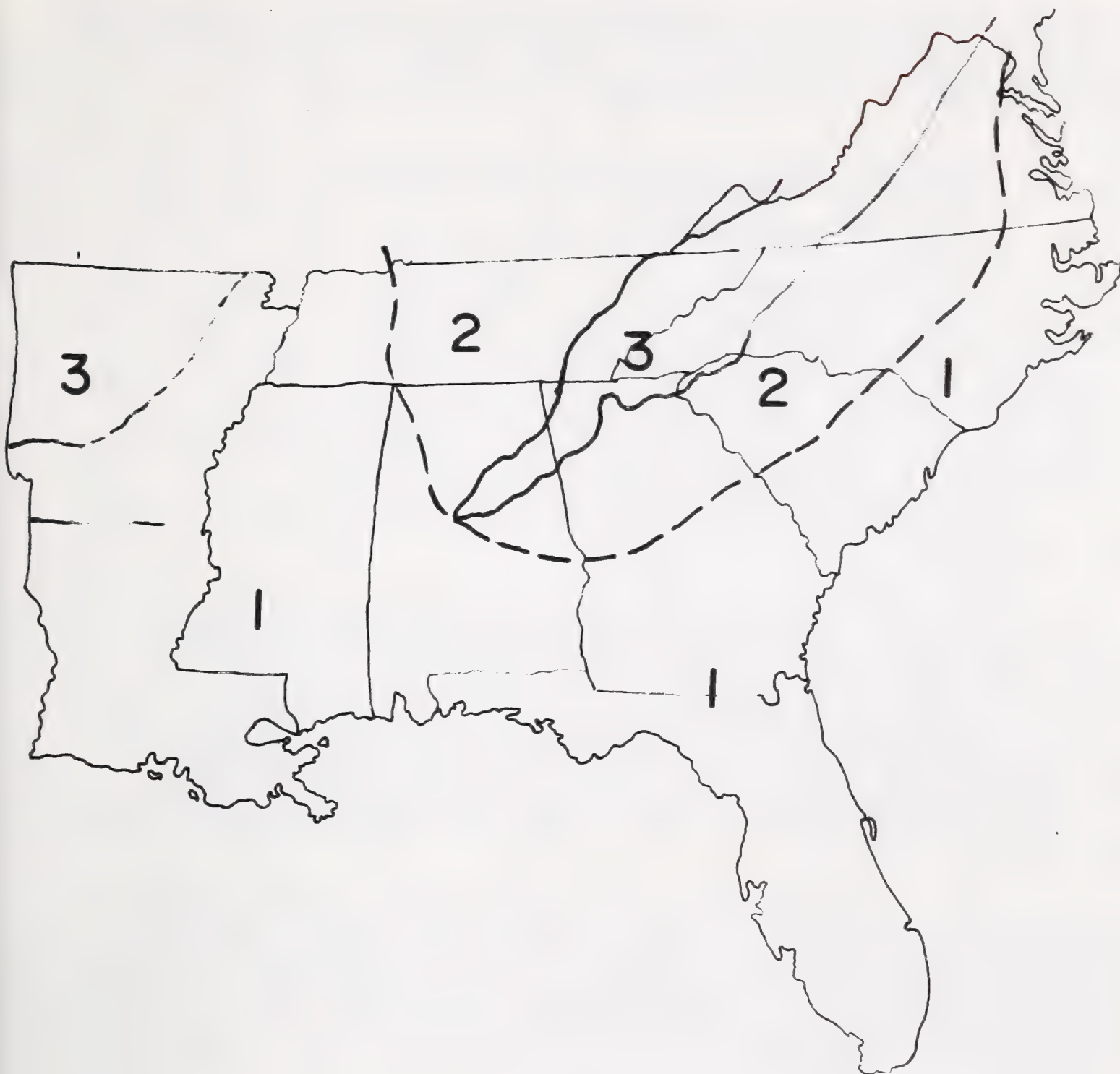


Figure 1.--Physiographic provinces of the Southern States: 1. the Coastal Plain; 2. the Piedmont, including the interior plateaus; 3. the Mountains, including the Blue Ridge, Ridge and Valley Area, and Ozark Plateau (after Braun 1950).

represent the full range of fire frequencies and intensities. Because fires are more frequent and better studied in the Coastal Plain, the discussion will be biased towards this province. After reviewing the variations in fire frequency and intensity, I shall consider the general causes and consequences of these variations.

VEGETATIONAL VARIATION AND FIRE IN THE SOUTHEAST

General Environmental Patterns

From the Coastal Plain, across the Piedmont to the mountains, the climate becomes increasingly continental and the lengths of growing seasons decrease. However, within these physiographic provinces, climate varies considerably. The middle Atlantic region and mountains are temperate (with a growing season of 150-250 days) while the more southern Coastal Plain and Piedmont are warm temperate to subtropical with growing seasons exceeding 350 days along the Gulf of Mexico. Precipitation, mostly as rain, varies between 1 000 and 1 500 mm and occurs year-round, frequently with a late summer peak. This summer peak is accentuated in the gulf States where moderate winter drought is common. In the middle Atlantic region, 2-4 week droughts are most common in spring and autumn. It is during these drought periods that fuel and moisture conditions are most favorable for fire.

As their names suggest, these provinces vary considerably in topography. The lower Coastal Plain (younger terraces) is characterized by low relief and complex hydrologic patterns (Murray 1961). In this area, braided streams and swamps are common and the mean water table frequently is at or just below the soil surface. A change in soil surface elevation of less than 1 m can, thus, determine whether an area is perennially flooded or comparatively dry. On the upper Coastal Plain, composed of older terraces, erosion has created a more piedmont-like topography and exposed older sediments. The Piedmont gradually increases in elevation to the mountains with a rolling hill type topography. The topography of the mountains, of course, represents the greatest diversity and relief.

The soils of much of the Coastal Plain have only recently evolved from late Tertiary and Quaternary sediments. Entisols (soil with no profile development), particularly quartzipsamments, are typical of dryer "upland" areas whereas histosols (organic soils) characterize perennially moist areas. Ultisols, particularly reduced gleys (umbraquits and ochraquits), have developed from sedimentary silts and clays in areas of intermediate drainage (Buol 1974). Regardless of soil type, Coastal Plain soils are comparatively infertile. The ultisols of the Piedmont represent some of the oldest soils in the world. Although these soils are potentially fertile, erosion and poor farming practices have reduced their productivity severely in many places (Coile 1940). Due to topography, soils of the mountains are shallow and poorly developed (inceptisols).

Coastal Plain

XERIC SANDHILLS AND SAND-PINE SCRUB

Perhaps the most peculiar of all ecosystems in the Southeast are those that occur on the well-drained sands. Despite rainfall in excess of 1 000 mm/yr, rapid drainage results in quite xeric conditions, particularly for plants rooted in the upper soil horizons. High radiation due to sparse canopy cover and high soil albedo further exacerbate this situation.

On floristic and physiognomic grounds, these ecosystems can be divided into two distinct groups, the sandhill longleaf pine-turkey oak forests and the sand-pine scrub (Laessle 1958). The understory in the former is characterized by a sparse cover of herbs, particularly grasses, whereas that of the latter is dominated by shrubs.

The longleaf pine-turkey oak forests are characteristic of sandhills extending along the Coastal Plain-Piedmont fall line from the Carolinas to Alabama. Similar forests are characteristic of other elevated sandy areas such as the sand rims associated with the Carolina Bays and ancient shoreline deposits. Today, these areas support scattered longleaf pines (Pinus palustris),^{1/} with an understory of turkey oak (Quercus laevis), sand oak (Q. pumila), persimmon (Diospyros virginiana), scattered clumps of wiregrass (Aristida stricta), and a variety of drought-adapted herbs (Wells and Shunk 1931). With somewhat more favorable moisture conditions and infrequent fire, pine density increases and other hardwoods become frequent including Q. margaretta, Q. marilandica, and Liquidambar styraciflua.

Fire frequency in these ecosystems is related in large part to fuel accumulation. In some areas sufficient pine litter and ground fuel accumulates within a 3-to 5-year period to carry low intensity fires. In these areas prescribed fires are applied to control the growth of hardwood species. In the driest sites, such as on the coarse sand rims of the bay lakes, 30 to 40 years may be required to accumulate sufficient fuel for a fire. Most of the accumulated fuel is in the form of scattered hardwoods and some shrubs so that when fires do occur in these areas, they may be quite intense. In many areas the structure and composition of these ecosystems may be an historical artifact reflecting past abuses. Many areas now dominated by very scattered pines and xeric oaks were once dominated by denser pine overstories with sparser hardwood understories (Bartram 1791, Wells and Shunk 1931). Many of the pines were harvested or otherwise killed during a long period of turpentine operations (Ashe and Pinchot 1897). It is not unusual to find scattered gnarled 200-year-old longleaf pines on the most xeric sand rims which still bear the scars of past turpentine extraction. Since fire frequency in these areas depends on the accumulation of ground fuels, particularly pine needles in areas lacking wiregrass, it seems reasonable to conclude that the removal of pines directly resulted in decreased fire frequency. Once established, this longer fire cycle will be maintained since it favors the growth of hardwoods and retards invasion and establishment of longleaf pine which depends on frequent fires. Thus, flammable fuels are slow to accumulate.

The sand pine scrub is characteristic of the nutrient deficient sands of the relict Pleistocene shorelines of peninsular Florida. The dominant tree in this community is sand pine (Pinus clausa) with a scattered shrubby understory, several shrubby live oaks, turkey oak, saw palmetto (Serenoa repens), and fetter brush (Lyonia spp.) (Mulvania 1931, Kurz 1942, Laessle 1958). Kurz's (1942) suggestion that these scrubs developed from longleaf pine-turkey oak communities seems unlikely (Laessle 1958). Harper (1914) and Laessle (1958) emphasized the potential role of fire in maintaining this community.

In contrast to sandhill forests, the fire cycle in scrub-pine forests corresponds to the longevity of the sand pine, i.e., 30 to 60 years (Webber 1935, Harper 1940, Laessle 1965). Since sand pine seedlings successfully establish only after fire, such forests are even-aged (Laessle 1965). Sand pine has moderately serotinous cones and adult trees sprout epicormically. As one might expect, the shrub species in this community also sprout vigorously following fire.

The comparison of sand pine scrub and sandhill forests emphasizes the potential for vegetational determination of characteristic fire frequency and intensity regardless of general climatic and edaphic conditions. Presumably, the low-nutrient conditions of the relict shoreline sands of Florida favor growth of shrubs over herbs (Laessle 1958). Low rates of fuel accumulation in addition to low fuel flammability diminish fire probability. Fire frequency would, thus, be related to the frequency of dry conditions sufficient to increase shrub flammability and fuel accumulation sufficient to perpetuate a fire (Hough 1973). Unlike those fires in the sandhills, fires in this ecosystem burn

^{1/}Nonmenclature according to Radford and others 1968.

virtually all aboveground material. It is not surprising that the successional patterns and life-history characteristics of the component populations relative to fire differ between these ecosystems.

SAVANNAS

Progressing toward moister conditions, the sandhill vegetation is floristically continuous with the savannas of the Coastal Plain (Wells 1928, Wells and Shunk 1928). Many sandhill species are also important savanna dominants and the main vegetational change with increased moisture is increased total plant cover and species diversity. These ecosystems are physiognomically characterized by scattered trees and abundant graminoids. Longleaf pine is the most common tree; however, loblolly pine (Pinus taeda), slash pine (P. elliotii), and pond pine (P. serotina) may also occur. Tree productivity is moderate to poor, and apparently limited by nutrient availability (Pritchett 1977). Understory grasses and sedges include wiregrass, broomsedge (Andropogon spp.), Ctenium aromaticum, Carex spp., Fimbristylis spp., and Rhynchospora spp. In the richest areas, these communities rank second in diversity of herbs only to the southern Appalachian cove forests. Included among the herbs is a diverse assemblage of insectivorous plants such as Dionaea muscipula (North Carolina), Drosera spp., Pinguicula spp., and Sarracenia spp.

Soils in savanna areas vary from sandy entisols, characteristic of more xeric areas, to heavier ultisols in moister sites. They are relatively infertile, particularly with respect to nitrogen and phosphorus (Metz and others 1961, Wells 1971, Christensen 1977a). These nutrient-poor conditions result from a combination of low soil adsorptive capacity, reducing environments, and slow rates of decomposition and mineralization.

In general, floristic diversity of savannas is highest in more southern latitudes, probably reflecting more favorable year-round growing conditions. In any local area, variations in species composition are generally related to moisture availability and fire frequency. On drier sites wiregrass dominates, frequently comprising over 95 percent of the total herbaceous biomass (Parrott 1967, Christensen 1977a). Other common herbs, particularly in recently burned areas, include several orchid species Dionaea muscipula, Polygala spp., Rhexia spp., and a variety of composites. In areas unburned for 5 to 8 years, shrubs (including Myrica cerifera, Ilex spp., and Vaccinium spp.) and the hardwood trees (including Diospyros virginiana and Quercus spp.) become more frequent. In moister savannas the diversity of graminoids is considerably higher, including more members of the Cyperaceae and Juncaceae.

The role of frequent, low-intensity fires in the maintenance of these savannas is well known. The understories of permanent plots in savannas protected from fire 4 to 8 years at the Tall Timbers Research Station, Tallahassee, Fla., are now dominated by thickets of hardwood trees and shrubs (Kurz 1944, Komarek 1977). Future fires in these plots will obviously be considerably more intense. In the Green Swamp of southeastern North Carolina, moist savannas protected from fire are invaded by a variety of shrub species (typical of the adjacent evergreen shrub bogs (Wells and Shunk 1928, Kologiski 1977)).

The potential importance of fire in affecting plant-pathogen or plant-herbivore interactions is seen in savanna. Seedlings of longleaf pine may become infected with a fungus, Schirrhia acicola, which causes "brown spot" disease. In the absence of fire, this fungus severely retards growth and kills many infected seedlings (Siggers 1944, Wakeley 1970, Boyer 1975). Fire effectively controls fungal growth and subsequent pine mortality and is, therefore, often prescribed in infected stands.

In the Carolinas, the transition from moist savanna to evergreen shrub bog may be very abrupt despite a more gradual gradient in soil moisture conditions. Although the occurrence of species in either the savanna or bog certainly reflects differing competitive abilities along this moisture gradient, the precise location and abruptness of the ecotone is a function of fire. Frequent surface fires (every 1 to 5 years) prevent invasion of shrubs into moist savanna microsites. These fires ordinarily stop at the shrub-bog margin due to the high shrub moisture content. It is therefore not surprising that the shrub species growing along the shrub bog-savanna ecotone are also characteristic of recently burned shrub bogs (Woodwell 1956, Christensen 1978).

The "natural" fire frequency for Coastal Plain savannas was probably once every 2 to 8 years. This estimate is based on the life histories of many of the dominant species (Wahlenberg 1946) and rates of fuel accumulation (Parrott 1967) which are discussed in another section of this paper. Within this range, the optimal fire frequency appears to vary with the environment. In moister, more productive areas (either due to soil or climate) the herbaceous understory is quickly replaced by hardwoods. Long-term fire exclusion on these sites may result in eventual succession to hardwood forests as suggested by Wells (1928) and Quarterman and Keever (1962). Vogl (1973) notes that even a few years without fire results in the disappearance of prairie species from savannas of the Gulf States. On drier sites, fire exclusion for long periods is quite difficult and unburned areas simply decline in productivity (Parrott 1967, Christensen 1977a). With exception of the invasion of scattered shrubs, such areas show no signs of succeeding to hardwoods (Woodwell 1956, Kologiski 1977).

GRASS-SEDGE BOGS

Grass-sedge bogs occur infrequently throughout the Coastal Plain and appear to have multiple origins. Most sites are relatively moist and dominated by a variety of graminoids, herbs, and ferns. Some grass-sedge bogs originate from intensive cutting of moist savanna areas. Reestablishment of woody plants is slowed or halted by subsequent frequent fires (Wells and Shunk 1928, Cypert 1961, Kologiski 1977). Other grass-sedge bogs result from very intense fires during dry periods in areas of considerable peat accumulation. These fires may burn the peat below the mean annual water table creating a perennially moist depression which is rapidly invaded by herbs. Because the litter produced by these herbs is rather combustible, fires may be comparatively frequent. Thus, once established, grass-sedge bogs may be perpetuated by virtue of this change in fire frequency (Cypert 1961).

PINE FLATWOODS AND PALMETTO FLATWOODS

The flatwoods are differentiated from savannas primarily on physiognomic grounds. In general, tree density is considerably higher, often forming a nearly closed canopy. In the Coastal Plain of the Carolinas these forests are dominated by longleaf or loblolly pines with a few understory species shared with savanna or hardwood communities. From southern Georgia across the Gulf States, pine-palmetto flatwoods are common. On sandy, better drained sites, these woods are savanna-like, being dominated by grasses and sedges, scattered individuals of saw palmetto, and longleaf pine. These areas are typified by fire frequencies similar to savannas (Hilmon 1968). On heavier soils with poorer drainage, the understory is composed of a mixture of shrubs and saw palmetto and the overstory is dominated by either longleaf or slash pine. The shrubs include several live oak species, gallberries (Ilex coriacea and I. glabra), and wax myrtle (Myrica cerifera). Because of moister conditions and slower rate of flammable fuel accumulation, fires are less frequent than in graminoid-dominated ecosystems. However, the comparatively high flammability of the shrubs, shrub height, and heavy needle drape result in somewhat more intense fires (Hough and Albini 1978). As one travels north along the Coastal Plain the palmetto and live oaks disappear, but flatwoods with scattered wax myrtle and gallberry are common in the Carolinas on heavy soils.

The relative importance of loblolly pine versus longleaf pine in the northern Coastal Plain and slash pine versus longleaf pine to the south is to a very large extent a reflection of changes in fire frequencies and silvicultural practices. For example, fire suppression in the Francis Marion National Forest near Charleston, S.C., beginning at the turn of the century has resulted in the dominance of loblolly pine on some sites which formerly supported longleaf pine. Prescribed fire in these forests is now favoring longleaf reestablishment (Lotti and others 1960). In the palmetto flatwoods, fire protection has increased the dominance of slash pine, which was formerly confined to only moist sites (Little and Dorman 1954, Fowells 1968).

Although fires in flatwoods, particularly gallberry-palmetto type, are considerably more intense than those of savannas, they do not typically kill canopy trees (Hough and Albin 1978). Postfire revegetation is rapid with the shrubs sprouting from subterranean organs and the palmetto sprouting from prostrate stems (Hilmon 1968).

SHRUB BOGS

Shrubby, more or less evergreen ecosystems dominate many of the poorly drained interstream Coastal Plain terraces. Shrub stature in these evergreen shrub bogs or pocosins varies between 1 and 4 m. Scattered emergent trees, particularly pond pine (Pinus serotina), may reach 20 m. Other emergent trees found in shrub bogs include Acer rubrum, Gordonia lasianthus, Magnolia virginiana, Persea boronia, and Chamaecyparis thyoides. Shrub species include Lyonia spp., Cyrilla racemiflora, Kalmia spp., and Clethra alnifolia.

The soils of shrub bogs are histosols, organic soils representing in many cases peat accumulation in excess of 3 m (Wells 1946, Woodwell 1956, Kologiski 1977). Like other Coastal Plain soils, these peats are quite infertile; however, nutrient availability varies to some extent with hydrologic conditions. Shrub bogs in elevated, moor-type conditions receive no surface water and only nutrients provided by rainwater. These areas are typified by very stunted shrubby growth (frequently < 1 m tall) and low productivity. Because they are slightly elevated, they tend to dry out during drought periods.

The specific effects of fire and details of postfire ecosystem response remain unknown in this ecosystem. However, a few general trends are clear. Because of the shrubby character of the vegetation, shrub-bog fires are intense. Ordinarily all aboveground vegetation is burned, though not necessarily consumed. It is not unusual for the peat to remain unburned. However, if the fire is particularly intense, the peat may burn to the level of the water table or to mineral soil. Wells and Boyce (1953) speculate that exceedingly intense fires occurring in very dry years may have "opened" the shrub bogs occurring in elliptical depressions characterizing the Coastal Plain of the Carolinas, creating or recreating many present-day lakes.

Vegetational response following fire in evergreen shrub bogs is, in some ways, quite similar to that in the western chaparral. Pinus serotina produces moderately serotinous cones and reproduces successfully primarily after fire (Woodwell 1958). Furthermore, mature trees sprout vigorously from protected buds along the bole, main branches, and root crowns. Only in the most severe fires are they killed (Woodwell 1958). In addition, virtually all shrubs sprout vigorously from roots and rhizomes. Herbs, such as the ferns, Woodwardia virginica, Osmunda spp., and Pteridium aquilinum, as well as Carex walteriana, Lachnanthes caroliniana, Rhexia spp., and Sarracenia spp. are common immediately after fire (Woodwell 1956, Christensen 1978). Following low-intensity fires, the shrub composition basically reflects the prefire composition. However, if fires are sufficiently intense to kill dominant shrubs then faster growing shrubs such as Kalmia carolina, Zenobia pulverulenta, and Vaccinium spp. may initially dominate. These are eventually overtopped in the absence of fire by Lyonia lucida, Cyrilla racemiflora, and Ilex spp. (Wells 1946). Woodwell (1956) noted that shrub

diversity in many pocosins may be inversely related to productivity. He suggested that on poorer sites Lyonia and Cyrilla in particular are less able to dominate, thus favoring coexistence of more species.

Management and land use patterns in the past 200 years have influenced the development and maintenance of shrub-bog ecosystems. According to Ashe and Pinchot (1897) many present shrub bogs prior to settlement were cedar swamps dominated by Chamaecyparis thyoides. The frequency of young Chamaecyparis trees in some shrub bogs (Woodwell 1956) and the presence of large whitecedar logs beneath the surface peat of shrub bogs of southeastern North Carolina (Wells 1946, Kologiski 1977) support this notion. Korstian and Brush (1931) noted the paradox that Chamaecyparis trees are quite susceptible to fire, being killed by even low-intensity surface fires, but that successful seedling establishment occurred primarily after fire. Penfound (1952) therefore considered many of these shrub bogs to be part of a successional sere leading to cedar swamp forest. It should be noted, however, that Chaemaecyparis, as well as Nyssa spp. and Taxodium spp. are much more common in fen-type ecosystems than moors. Because the elevated shrub bogs dry more frequently, fires are sufficiently frequent to prevent establishment of less fire tolerant species. It is likely that management practices are retarding succession in fen-type sites. In many southeastern swamps, water tables have been successfully lowered for silvicultural and agricultural purposes. This change has undoubtedly increased the frequency of dry periods in affected shrub bogs and thereby increased the frequency of fire (Kologiski 1977). In many shrub-bog areas, prescribed fire is being used to control fuel accumulations and to improve silvicultural site conditions.

COASTAL PLAIN HARDWOODS

The occurrence of mixed deciduous forests, frequently dominated by beech (Fagus grandifolia) and Magnolia grandiflora, in areas of low fire frequency has been used as evidence that the "potential" or "climatic climax" vegetation in the absence of fire is a mixed hardwood forest (Harper 1911, Wells 1928, Kurz 1944, Quarterman and Keever 1962). As discussed earlier, ecosystems protected from fire on mesic sites are indeed succeeding from pine to mixed hardwoods (Blaisdell and others 1974, Hebb and Clewell 1976, Delcourt and Delcourt 1977). It should be noted that such hardwood ecosystems are associated with phosphatic and calcareous soils. It is doubtful that ecosystems typical of sandy or very nutrient-deficient soils or perennially moist soils will succeed to such a mixed hardwood community.

Oak-dominated forests characterize the elevated margins of many wetland ecosystems (Penfound 1952). Oak species include Quercus laurifolia, Q. phellos, and Q. nigra. These sites may be quite productive and have, in many locations, been converted to loblolly and slash pine plantations. In these areas fire is frequently used to prevent reestablishment of hardwoods.

At present, no information is available on the effects of fire in Coastal Plain mixed hardwood ecosystems, although it is probably reasonable to expect that fire response in these communities would be similar to that in the Piedmont deciduous forests discussed below. In general terms, fires are quite infrequent and their specific effects would undoubtedly depend on their intensity.

SWAMP FORESTS

The swamp forests of the Southeast represent a diverse assemblage of forest cover types united by the presence of perennially moist substrata (Penfound 1952). In areas where the soil is usually moist but standing water infrequent, Atlantic whitecedar forests are common. The understory in such areas is dominated by evergreen shrubs where soil organic matter is high and by a mixture of shrubs, loblolly pine, and scattered hardwoods on sites with mineral soils (Kologiski 1977). As mentioned

previously, whitecedar forests can hardly be considered stable in the absence of fire, yet even low-intensity surface fires kill adult trees (Korstian 1924, Korstian and Brush 1931). Seedling establishment appears to be confined to recently burned areas. McKinley and Day (1979) noted considerable germination of whitecedar seeds, as well as those of many herbs and shrubs, following fire in a whitecedar stand. Buell and Cain (1943) showed that in the absence of fire whitecedar forests would succeed to evergreen bay forests. These forests are therefore the product of a low-frequency, relatively high-intensity fire regime which is probably related to their marginally moist soil conditions. Too frequent fire, either prescribed or the result of lower water tables, will convert such areas to shrub bogs. However, infrequent fires result in decreased importance of whitecedar and pine.

Swamp forests are dominated by a mixture of deciduous and evergreen species which vary in dominance in response to hydrologic conditions, nutrient availability, and fire. In the areas of deepest flooding, Nyssa aquatica and N. ogechee are most common. Taxodium spp. and Nyssa sylvatica var. biflora dominate pond margins, wet runs, and lowland bays. Adult cypress trees are more resistant to fire than most swamp hardwood species. Thus, infrequent, low-intensity fires may increase cypress dominance. On sites where the main input of water is as rain and nutrients are presumably more limiting, evergreen species, such as Gordonia lasianthus, Magnolia virginiana, and Persea borbonia increase in dominance. These sites would be occupied by whitecedar forests or evergreen shrub bogs if fire frequency were increased. When fires do occur in swamp forests, however, the vegetational outcome is to a large extent a function of fire intensity and the level of the existing water table (Kologiski 1977, Cypert 1961). A shallow burn, that is one having little effect on the soil, would be revegetated by shrub bog or pocosin species which would, in the absence of further fires, succeed to cedar swamp. A deep burn in an area of high water table may initiate a sedge bog. Once established, frequent fires tend to maintain this open treeless vegetation indefinitely. This is probably the origin of the "prairies" and "houses" of the southern swamps, such as the Okefenokee (Cypert 1961, 1973). It is also possible that fires which substantially remove peat deposits in company with a lowering of the water table, could result in the establishment of deciduous swamp forests (Kologiski 1977).

Piedmont Forests

By 1840 most arable land on the southern Piedmont was under cultivation. Because of poor farming practices and economic conditions, much of this land was subsequently abandoned. Much of the Piedmont is recovering from this disturbance. The successional patterns following cropland abandonment have been described by Billings (1938), Oosting (1942), and Keever (1950). In general terms, herbs dominate during the first 10 years of the succession but are eventually shaded out by pines. Hardwood species successfully compete in the pine understory and eventually replace the pines to form a mixed hardwood forest. I will briefly discuss the characteristics and role of fire in each of these successional stages.

OLD FIELDS

Nearly all fires occurring in old fields are begun by man either accidentally or for the purposes of retarding succession (Odum and others 1974). Their net effect on the vegetation is to kill nearly all invading trees and shrubs and to enhance the growth of herbs. The specific environmental effects of fire causing the enhanced herb growth are probably varied (cf. Jordan 1965, Hulbert 1969, Old 1969, Peet and others 1975).

Perhaps a more central issue with regard to this symposium is why natural fire is unimportant in old fields compared to physiognomically similar ecosystems on the Coastal Plain. Three factors seem to be important: 1) isolation of old fields, 2) fuel moisture content, 3) accumulation of dead fuel. These are discussed in a later section.

PINE FORESTS

The pine forests of the Piedmont are dominated by mixtures of Pinus taeda, P. echinata, and P. virginiana and an understory of hardwoods. Although lightning fires may occur in this vegetation, most fires are of human origin. Prescribed fire is frequently used on a 4-to 5-year rotation to control the growth of understory hardwoods and improve pine productivity.

It is difficult to speak of natural fire frequencies in successional forests which may not have existed as such prior to extensive cultivation and abandonment. Whereas mature trees of all three common pine species can withstand low to moderate surface fires, they are killed outright by high-intensity fires. Thus fires in stands with considerable understory development may potentially be devastating.

Oosting (1944) and Oosting and Livingstone (1964) compared the effects of surface and crown fires in a 35-year-old loblolly pine stand 9 years and, again, 29 years after fire. At 9 years pine basal area was reduced slightly by the crown fire and virtually all pines had been killed by the crown fire. However, pine regeneration on the burned area was dramatic resulting in a ninefold increase in pine density after 29 years. Although hardwood sprouts were numerous in the crown-fire area at 9 years, they were subsequently overtopped by pines resulting in reduced hardwood cover compared to either the unburned area or surface-fire area. Although the pine overstory suffered less immediate impact from the surface fire, subsequent mortality, perhaps from pathogens invading fire scars, resulted in a marked decrease in pine density and basal area to the benefit of the hardwoods. These data suggest that infrequent, but intense crown fires could result in long-term perpetuation of loblolly pine forests, whereas infrequent low-intensity surface fires may speed succession to hardwoods.

It appears that the most significant factor affecting fire frequency in Piedmont forests is fuel moisture content. Understory vegetation and litter is frequently too moist to carry a fire. This is largely the result of heavier soils which retain water near the surface keeping fuels moist. Thus, as with moist Coastal Plain ecosystems, the probability of fire is the product of the probability of an incendiary event and the probability of dry fuel conditions.

BROADLEAVED DECIDUOUS FORESTS

The deciduous forests over much of the Piedmont and lower mountain slopes are dominated by a variety of oaks and hickories (Oosting 1942, Braun 1950). White oak (Quercus alba) is particularly important, comprising 40 to 70 percent of the basal area of many upland forests. On moist slopes or alluvial sites, the most common hardwoods are sweetgum (Liquidambar styraciflua), tulip tree (Liriodendron tulipifera), beech (Fagus grandifolia), and sugar maple (Acer saccharum var. floridanum).

Although very little research has been done on fire effects and response in Piedmont hardwood stands, several lines of evidence suggest that past fires may have significantly influenced deciduous forest composition and that the lack of fire may be significantly influencing it today. As already discussed, presettlement records indicate that Piedmont forests were considerably more open, perhaps even savanna-like, presumably maintained by frequent burning by Indians. Such a fire regime would have selected for more fire-resistant hardwood species. Assuming this to be the case, it should not be surprising that larger size-class upland oaks and hickories

considerably more resistant to fire than hardwood species typical of moister environments. It seems logical to presume that fires would be infrequent in these moister areas.

Examination of the population structures of many hardwood species suggests that major periodic disturbance is essential for long-term maintenance. Size-class distributions of oaks and hickories in many upland sites show a consistent underrepresentation in the sapling and small tree size classes because of high seedling mortality (Keever 1973, Christensen 1977b, Harcombe and Marks 1978). Furthermore, this trend is most evident among species typical of upland or dry sites where fires are apt to be more frequent (Harcombe and Marks 1978). It would appear that in the absence of disturbance successful reproduction of these species is unlikely. Hurricanes, as well as fire, may be important in this regard. Size-class distributions in an oak-hickory forest 36 years after burning show considerably more recruitment among major hardwood species than in an adjacent unburned part of the same stand (Christensen unpublished data).

Notwithstanding indications that fire may influence deciduous forest composition and structure, it obviously upsets ecosystem functioning to a much greater extent than in plant communities where fires are more frequent, predictable, and less intense. Compared to the more open forests of the 17th century, fires in existing deciduous forests tend to be quite intense and destructive unless carefully managed. Even low-intensity surface fires may wound many trees making them susceptible to attack by pathogens. Hodgkins (1958) points out that the specific impact of fire in deciduous forests is very dependent on the season of burning, with summer fires being most intense and having the greatest effects.

Mountains

To a large extent the effects of fire in the higher elevation vegetation of the southern Appalachians are similar to those for more northern climes discussed by Dr. Heinselman in this volume. Here I will confine my comments to two ecosystems unique to the southern Appalachians and perhaps representing extremes with regard to fire influence. These are the mixed mesophytic or cove forests and the grass balds.

The cove forests are considered by many to be the mother lode of tree diversity for the entire eastern deciduous forest (Braun 1950, Whittaker 1956). Among the reasons cited for their comparatively high species diversity is the apparent lack of disturbance. Recent evidence indicates that relatively intense, but very infrequent, disturbances may also contribute to this diversity. Many of the dominant cove forest trees are relatively intolerant of low light conditions. Lorimer (1976) found that age-class distribution of such species in the Joyce Kilmer Memorial Forest were multimodal and that the modes over a 400-year period correspond to known disturbances, particularly fire and hurricanes. Such disturbances at any location were very infrequent (once every 200 to 400 years).

For the past 30 years ecologists have argued over the origin of and factors maintaining the grass balds or meadows of the southern Appalachians. Some of the argument appears to stem from their probable multiple origins. The higher elevation balds appear to be relics of vegetational shifts associated with climatic change over the past 6,000 years (Mark 1958). The lower elevation balds and ridgetop balds of Shenandoah National Park appear to be anthropogenic (Wilhelm 1973). In nearly all cases these balds or meadows are being invaded by woody vegetation--rhododendron, spruce, and fir at the higher elevations and shrub species at lower elevations (Gersmehl 1971). The rate of this encroachment is greatest at lower elevations. Fire has been frequently cited as an important factor maintaining the balds (Wells 1936, Wilhelm 1973). Recent studies by Barden (1978) and Cocking (1978) verify the effectiveness

of fire in maintaining open balds. In this particular case, the optimal frequency varies with bald elevation. Low elevation balds are quite productive and invasion is rapid. Annual or biennial fires are necessary (Wilhelm 1973), whereas higher elevation balds would be expected to have slower rates of fuel accumulation and encroachment and therefore would persist where fire was less frequent.

PAST HISTORY OF FIRE IN THE SOUTHEASTERN UNITED STATES

All available data suggest that fires were influencing southeastern ecosystems throughout the Quaternary. However, there are also indications that fire frequency and intensity varied considerably during this period.

Although charcoal fragments are distributed throughout pollen and peat profiles taken from various locations on the Coastal Plain of the Carolinas (Buell 1945, 1946; Frey 1953; Whitehead 1967), more recent sediments (i.e., ca. 7,000 years BP to present) contain more charcoal. Buell (1946) noted a very abrupt transition in quantity of charcoal corresponding to an equally abrupt change in pollen rain. The lower peat layer with moderate amounts of charcoal contained pollen of spruce (*Picea* sp.) and jack pine (*Pinus banksiana*) or red pine (*P. resinosa*). This suggests that the vegetation during post-Wisconsin glacial was similar in some respects to boreal forests. Watts (1980) suggests that the vegetation at this time was a mosaic of pine and spruce stands with prairies and sand-dune vegetation. Pollen in the upper layers of this profile (which contained considerable charcoal) was representative of present-day pollen rain in this area. Buell attributed this differential distribution of charcoal to interrelated changes in climate and vegetation and to the advent of man.

Peat and sediment cores from the Gulf States indicate that most of the present-day dominant species, and presumably the ecosystems they represent, were also present during the Wisconsin and immediate post-Wisconsin periods (Davis 1946, Cohen 1973, Delcourt 1978). Again, abundant charcoal indicates the presence of fire in these southern ecosystems. These data do, however, indicate localized variations in fire frequency associated with vegetational shifts and climatic change. For example, Cohen (1973) attributed variations in charcoal accumulation among peat profiles taken from various locations in the Okefenokee swamp to changes in fire frequency associated with changing vegetation patterns. Delcourt (1978) observed variations in charcoal accumulation along a profile from Goshen Springs, Ala., extending back in time beyond the range of carbon dating. They found that periods of high charcoal accumulation coincided to prevalence of pollen of more xeric elements whereas low charcoal correlated with pollen of mesic species. It appears likely that long-term shifts in climate resulted in interdependent changes in fire frequency and vegetation.

One unifying theme of journals documenting expeditions through the Southeast prior to 1800 was the high fire frequency (Bartram 1791, Catesby 1754, Lawson 1714, Maxwell 1910). In nearly every case Indians are blamed for the frequent fires. Descriptions of forest structure on both the Piedmont and Coastal Plain indicate rather open forests with a sparse understory and, at least in some areas, considerable herbage (Maxwell 1910, Bromley 1935) including many prairie species (Vogl 1973). Such areas may have had a savanna-like aspect, considerably different from their present-day physiognomy. This structure was presumably maintained by fire. The extent of these influences is difficult to judge since the accounts of early explorers hardly represent random or unbiased samples. The presence of the woodland bison as far south as South Carolina in the 18th century suggests that many areas of the Piedmont were indeed open and provided suitable range for these large herbivores (Maxwell 1910).

Analysis of early 19th century survey records from Louisiana and northern Florida reveal that fires were, in general, more frequent than they are today (Delcourt 1976, Delcourt and Delcourt 1977). This change in fire frequency has resulted in a shift

in dominance from pines to hardwoods on drier sites and from magnolia-beech to mixed hardwood dominance on mesic sites (Quarterman and Keever 1962, Blaisdell and others 1974, Hebb and Clewell 1976, Delcourt and Delcourt 1977).

FACTORS CONTROLLING FIRE FREQUENCY AND INTENSITY

Ignition Sources

Lightning is by far the most important natural cause of fire and the Southeast has the highest incidence of thunderstorms of any region in North America (Komarek 1968). Therefore, it seems paradoxical that the actual number of lightning fires is 3 to 5 times higher in the Rocky Mountains and Pacific States and that only 2 percent of the wildfires in the Southeast are caused by lightning (Taylor 1974). Although fires will not start without an ignition source, it is clear that successful ignition depends on other factors as well.

While the distribution of lightning is relatively uniform over the Southeast, the percent of fires caused by lightning is highest in the mountains (Barden and Woods 1974). This is true even though total number of fires is much higher on the Coastal Plain. Nonetheless, variations in number of lightning-caused fires appear not to be related to variations in thunderstorm activity but rather the presence of conditions conducive to ignition. Over the entire United States only 0.05 percent of lightning strikes actually result in fire. Presumably because of different fuel and climatic conditions, this value is maybe two orders of magnitude lower in the Southeast (Taylor 1974).

As discussed earlier, explorers such as Catesby and Bartram emphasized the fire management activities of Indians. Buell (1946) suggested that the increased frequency of charcoal in peat profiles since the Wisconsin glacial might be related to colonization of the Southeast by Indians. Today, areas of highest wildfire frequency often coincide with areas of high population density (Doolittle 1977). Obviously, man has locally increased the frequency of fire in many localities.

Fuel Moisture Content

Unlike much of the mid- and far West, precipitation in the Southeast is approximately equal to or greater than evaporation rates. Vegetation and ground fuels are, therefore, often too moist to carry a fire (Byram 1959). Indeed, this factor alone severely restricts the number of days available in a year for prescribed burning.

Variations in fuel moisture content contribute greatly to variations in fire frequency and intensity in the Southeast (Blackmarr 1972). Although rainfall is high, rapid drainage through the sandy soils of the Coastal Plain results in more rapid drying of ground fuels. The importance of fuel moisture content is demonstrated at the ecotone between savannas and shrub bogs where frequent savanna fires are abruptly stopped at the bog margin. As discussed previously, such fires tend to sharpen this ecotone. Only during periods of prolonged drought do fires continue into the shrub bogs. The frequency of fires in these pocosins is largely determined by the frequency of such droughts. Where water tables have been artificially lowered, fire frequency has increased, perhaps maintaining shrub bogs in areas formerly vegetated by cedar swamp forest.

Water retention characteristics of the soils may be responsible in part for reduced fire frequency on the Piedmont compared to the Coastal Plain. Piedmont soils are generally heavier and retain more water near the surface. This results in higher moisture content of surface fuels.

Environmental Mosaic

The frequency of fire at a particular location is often a simple consequence of the topographic and vegetational conditions adjacent to that location. That is to say, the likelihood of a fire in a given forest stand is not just dependent on the frequency of ignition events in that stand, but also on the likelihood of fire moving in from neighboring stands. The influence of variations in fire spread on vegetational patterns was first documented by Harper (1906, 1911) as being responsible for "islands" or "hammocks" of broadleaved forest in areas dominated by fire-maintained pine communities. Variations in topography along with moisture conditions seem to account for the presence of mixed hardwood and beech-magnolia forests along the Gulf Coast (Kunz 1944, Blaisdell and others 1974). Although no information is available on this point, it seems possible that small isolated areas environmentally suitable for the establishment of savannas, for example, would not have the same fire frequency as environmentally similar areas contiguous to large expanses of savanna. Perhaps the physiognomic uniformity of large areas of the Green Swamp is, in part, related to this effect.

Over the past 50 years artificial firebreaks, both intentional and unintentional, have become a dominant part of the southeastern landscape. Annual, low-intensity prescribed fires are applied throughout the Southeast to control wildfires. Furthermore, the patterns of agriculture, urbanization, and transportation dissect the environment forming effective barriers to fire spread. While fire frequency calculated as number of fires per year has remained relatively constant in the Southeast, total burned acreage is actually declining (Doolittle 1969, 1977). Therefore, fire frequency estimated on the basis of the number of times a particular tract of land is burned in a given time period is actually decreasing. In urban areas, fire suppression obviously has contributed to this trend but in the rural areas of the Coastal Plain and the mountains fire size is frequently controlled by the environmental mosaic and artificial fuel breaks such as roads (Barden and Woods 1974, Kologiski 1977).

Fuel Characteristics

Another factor contributing to variations in frequency and intensity of fire among southeastern ecosystems is variations in rates of fuel accumulation, fuel flammability, and fuel structure.

The rate of fuel accumulation in any particular ecosystem is a simple result of the difference between rates of production and decomposition. In many areas characterized by relatively frequent fires, the litter and detritus produced is often decomposed very slowly. A large proportion of the mineralization in these systems is accomplished as a result of fire. The reasons for slow rates of litter decomposition are varied. The foliage of many Coastal Plain plants, including pines, shrubs, and herbs, is quite sclerophyllous, containing large quantities of cellulose and lignin (Wells 1942). Although such sclerophylly is most intense in species with persistent evergreen leaves, it is found in many deciduous species as well. Although the selective forces for such sclerophylly may be varied (Caughey 1938, Monk 1965, Schlesinger and Chabot 1977), nearly universal consequences are reduced rates of decomposition and increased litter accumulation. These dead fuels, when dry, are quite flammable and their continued accumulation increases the likelihood of fire. Furthermore, this fuel mass frequently represents a substantial nutrient reservoir in otherwise nutrient-limited ecosystems. For example, living and dead surface fuels in pine-wiregrass savannas approach a steady-state mass of about $1\,000\text{ kg ha}^{-1}$ 4 years after fire. Subsequently, the total mass remains constant while the living component diminishes reflecting decreased productivity (Parrott 1967). Each year fires become more likely. Similar trends characterize other Coastal Plain ecosystems such as shrub bogs (Schlesinger 1978) and flatwoods (Hough and Albini 1978).

It is well known that the chemical composition of plants greatly affects their flammability. Although certain Coastal Plain shrubs, such as Myrica cerifera, Ilex spp., and Persea borbonia, are known to contain large quantities of aromatic compounds and are quite flammable (Rundel 1980), there has been no systematic study of plant chemical composition and flammability in the Southeast. Many Coastal Plain trees and shrubs produce tissues with comparatively high caloric values (Hough 1969) which may reflect higher quantities of flammable compounds.

The intensity of fire in a particular ecosystem is frequently a consequence of fuel structure. In forest with widely separated strata, such as savannas or frequently burned pine woods, fires are easily confined to the ground. However, in ecosystems with a more continuous vertical distribution of fuel, as in shrub bogs or long-unburned pine stands, fire frequently involves the crowns. Such vertical stratification may involve dead fuel (e.g., needle drape) as well (Wahlenberg 1960).

CONSEQUENCES OF VARIATIONS IN FIRE FREQUENCY AND INTENSITY ON SUCCESSIONAL PATTERNS

For years reviewers have suggested (Gleason 1939, Connell and Slatyer 1977), that community change is largely a consequence of changes in component populations. It would be futile to try to understand the effect of varying fire frequency and intensity on postfire successional patterns without also considering the impact of these variations at the population level. In this respect, fire responses are to a great extent determined by the role fire has played in the evolution of species life-history characteristics.

Fire is usually considered to have the most devastating effect in those ecosystems where it is infrequent and intense. Such systems in the Southeast include mesic deciduous forests, particularly the cove forests and swamp forests. It is in these communities that succession most closely approximates the classical paradigm of Clements (1916) and Odum (1969). The postfire environment is generally less favorable to the former residents and more favorable to a variety of pioneer species. Fire in such ecosystems may result in higher rates of erosion and nutrient loss compared to prefire conditions. While net primary production may increase, gross production is usually lower than in the mature forest. Although fire may play a significant role in the development of such ecosystems, one would hardly view it as a homeostatic mechanism. Fire occurrence in these ecosystems is related to the chance co-occurrence of an ignition source and suitable weather conditions rather than internal trends in the vegetation which increase fire probability. In this context fire may indeed be analogous to an injury from which the ecosystem must recover.

I should emphasize that the above situation is characteristic of the most moist and mesic environments, and that the specifics of plant response would depend greatly on fire intensity. As proposed by Kologiski (1977), plant response following fire in swamp forests varies with fire intensity, the most intense fires resulting in the most pioneerlike postfire vegetation. Thor and Nichols (1974) indicate that low-intensity surface fires even in relatively mesic hardwood forests may have relatively little environmental impact other than altering understory composition.

As stated earlier, increase in fire frequency may directly alter community structure and composition either by selecting fire-tolerant species or species which compete effectively in the postfire environment. As discussed earlier, increased use of fires by Indians probably contributed to the prevalence of shade intolerant oak species, particularly white oak, in upland Piedmont forests (Thor and Nichols 1974, Christensen 1977b). Infrequent fire appears to be essential for perpetuation of cedar swamp forests. Although such species do not have their life cycles obligately tied to fire, and may even be quite sensitive to fire, they depend on relatively open environments for successful reproduction. Fire is one of several types of disturbance which can enhance their success.

Successive fires in deciduous and mesic pine forests tend to become less intense due to changes in fuel quality and reduction in fuel quantity. As I have already noted, Piedmont forests of the 17th century may have been considerably more savanna-like with prairie grasses common in the understory (Vogl 1973). This condition would have arisen only after repeated fire. Once established, however, these conditions would enhance the probability of more frequent, low-intensity fires.

At the other end of the spectrum from the mesic forests are the fire-dominated communities of the Coastal Plain. The long-term perpetuation of evergreen shrub bogs, sand-pine scrub, flatwoods, and savannas is tied to fire. Although mean fire frequency and intensity may vary among these ecosystems, fire is a regular, almost predictable, phenomenon in each one. Successional trends in these communities are, in several respects, the opposite of traditional models. Species diversity is, for example, highest immediately following fire in these ecosystems and generally decreases, in some cases dramatically, thereafter (Wells 1942, Garren 1943, Woodwell 1956, Roberts and Oosting 1958, Lewis and Harshbarger 1976). Gross and net primary production are frequently highest in the first postfire growing season and decrease subsequently (Parrott 1967, Hilmon 1968). Many of these changes are attributable to increased nutrient availability and mobilization (Wells 1971, Jorgensen and Hodges 1971, Christensen 1977). The fire cycle may be viewed as a homeostatic process in such communities in which decreased productivity and dead fuel accumulation increase fire probabilities, thereby determining relative fire frequencies.

A common denominator in these systems is that sexual and vegetative reproduction of many species is directly tied to fire. Furthermore, the postfire vegetation is frequently dominated by the propagules and sprouts of the prefire dominants. The generally poor site conditions greatly reduce the likelihood of successful reproduction in interfire years (Wells 1942, Garren 1943, Wahlenberg 1946, Roberts and Oosting 1958, Christensen 1977) thereby selecting for life-history characteristics which concentrate reproduction in immediate postfire years. Although heat stimulated germination has been observed in some southeastern legumes (Cushwa and others 1968), fire stimulated flowering seems much more common, particularly in savannas. In some cases, such flowering response may be a physiological response to increased resource availability, in others fire is simply a triggerlike stimulus. In wiregrass (Aristida stricta), for example, clipping or burning will stimulate flowering (Parrott 1967), although seed production is an order of magnitude greater in burned compared to clipped areas (Christensen 1977).

The relationships between variation in fire frequency and intensity and species life-history patterns are perhaps clearest among the pines. The essential role of frequent fire to the growth and development of longleaf pine has been known for decades (Chapman 1932, Wahlenberg 1946). This pine does not have serotinous cones, nor does it produce epicormic sprouts. Its relatively large seeds germinate and establish best on postfire mineral soil. Resources during its next few years are allocated primarily to the roots (particularly a deep taproot) while the bud is protected by a sheaf of long needles and fire resistant scales. When the seedling attains sufficient size (usually 3 to 5 years, Allen 1964) it rapidly puts on apical growth so that in 3 to 4 years the sensitive apical bud is high enough to avoid damage from the relatively low-intensity surface fires. In an ecosystem with high-frequency low-intensity fires, the central evolutionary challenge for large woody plants is to grow from a seedling to a sapling sufficiently large to avoid fire damage. Because fires are low intensity, there has been no selection for sprouting; trees are rarely damaged. Furthermore, in environments where fires are quite frequent (in the case of savannas, every 4 to 8 years) serotinous cones provide little advantage and could be a real disadvantage since the individual with serotinous cones would miss nonfire or nearby-fire reproduction opportunities.

In contrast, the sand pine (*Pinus clausa*), pitch pine (*P. rigida*), and pond pine (*P. serotina*) sprout epicormically and show varying degrees of serotiny. All of these pines are typical of shrubby ecosystems which burn with high intensity at intervals of 10 to 30 years (Lutz 1934, Wells 1946, Laessle 1958). Survival of individuals from one fire to the next thus depends on their sprouting ability. Furthermore, seedling survival in interfire years is extremely improbable in these communities (Woodwell 1958) thus selecting for serotiny. In most cases, such serotiny is ephemeral (cones remain closed 5 to 8 years) thus maintaining a reservoir of seeds on the trees at any time, but also releasing some seeds each year which may successfully establish in other nearby disturbances. Considerable genetic variation exists among populations of all of these pine species with regard to the degree of serotiny (Fowells 1968). This suggests different patterns of selection within each species.

If a species' life history is partially or completely dependent on fire, any influence that plant had on the ecosystem that increased fire likelihood and maintained optimal fire frequency and intensity should increase individual fitness. This is the basic premise of Mutch's (1970) wildland fire hypothesis--that the evolution of fire-related plant life histories occurred concomitantly with the evolution of plant characteristics which increased flammability. It is difficult to find rigorous proof for this attractive idea, but changes in a number of Coastal Plain species following fire seem supportive. The presence of flammable aromatic compounds in some Coastal Plain shrubs may be a response to such selection. The accumulation of the dead leaves of wiregrass about the base of each plant render dry savanna areas virtual tinderboxes after 3 to 4 years. The production of relatively nondecomposable litter in many Coastal Plain plants may be a response to selective pressure such as that described above, though the hypothesis of "coevolution" of fire regime and species life histories seems impossible to test.

Back when the terminology was in vogue, ecologists such as B. W. Wells and Roland Harper viewed much of the Coastal Plain as a "fire prisere" and communities such as savannas and pocosins as fire "subclimaxes" (Harper 1914, Wells 1928). Fire in this view served as a force to halt succession along the sere towards the climatic climax. Although the concept of the climatic climax has lost favor, more recent workers have found it useful to view fire as a force inhibiting ecosystem development (Cypert 1961, Kilogiski 1977). If we were to start with a climax evergreen swamp forest, a low-intensity or "spotty" fire might result in the establishment of a pocosin or, perhaps, even a cedar swamp forest. However, an intense fire which burned deep into the peat might initiate a sedge bog. Thus, as successional theorists suggest, the degree of change resulting from a disturbance, i.e., fire, is largely a function of the intensity of the disturbance. The degree to which the ecosystem subsequently recovers to the climax state appears to be a function of subsequent fire frequency. As Cypert (1961) suggests, very frequent fires can in fact indefinitely maintain prairies or sedge bogs in previously forested areas. Less frequent fires can maintain pocosins (Wells 1946, Kologiski 1977) or cedar swamp forests (Cain and Buell 1943). As previously mentioned, environment and fuel characteristics in these seral communities may act to perpetuate fire frequency favorable to their maintenance. I should point out that both B. W. Wells and Roland Harper were aware of these relationships over 50 years ago (Harper 1914, Wells and Whitford 1976).

While this is a useful model with considerable pedagogical value, I feel it is also very naive and simplistic. It would be a mistake to say that if fire were removed from Coastal Plain ecosystems they would then necessarily continue along their successional way. There is little doubt that mesic savannas, particularly in the Gulf States, will quickly close in with hardwoods if not burned frequently. However, the pine-wiregrass savannas on sandy soils do not show similar tendencies. Whereas hardwood shrubs and small trees may become more prevalent in these areas in the absence of fire, large accumulations of dead ground fuel make the question of fire exclusion a moot point. Similarly, shrub bogs in many areas show no signs of having

ever been anything else or of becoming anything else in the absence of fire. While the absence of fire may mean continued succession in many cases, it simply results in stagnation in others.

SUMMARY

As anyone could have guessed, it is hopeless to try to develop a model to predict fire frequency and intensity based on a single factor. However, considering the chief factors affecting the likelihood of fuel igniting and the intensity with which it will burn, a few generalizations are possible: First, the greater the number of incendiary events, the greater the frequency of fire. Although variations in lightning frequency and characteristics may have some impact on fire frequency, human influences appear to be most important in this regard in the Southeast. In some areas man has decreased it by suppression, in others he has increased it by prescription and carelessness. In both cases, he has effected a great deal of vegetation change. Second, the continuity of the landscape also affects fire frequency by determining the characteristics of fire spread. It seems possible, even likely, that the number of fires per unit area per year may be higher today than ever, but even where such fires are allowed to burn, agriculture, roads, logging, etc., may prevent fire spread. Thus the fire frequency at any particular site may be reduced. Third, in general, drier conditions favor more frequent fires. Thus, lowering of the water table in areas formerly vegetated by cedar swamp forest may have permanently converted them to shrub bogs by increasing fire frequency. However, in the driest areas, such as sand ridges and sand-pine scrub, low rates of fuel production resulting in part from low water availability may decrease fire frequency. Fourth, the greater the rate of production of flammable fuel, the more frequently fires tend to occur. As previously discussed, this is a consequence not only of net production, but also rates of decomposition. It is possible, though this point is difficult to prove, that natural selection may actually favor the production of nondecomposable litter by plants as a means of assuring a fire cycle favorable to successful reproduction (Mutch 1970). The high frequency of fire in Coastal Plain ecosystems is a consequence of all of these factors.

The intensity of fire varies with respect to fuel quantity, water content, and structure. In those ecosystems where vegetational strata are widely separated, fires may be confined to the ground, whereas more continuous vertical distribution favors more intense fires. Stratification is frequently the direct consequence of frequent past fires.

Response to fire varies considerably according to the natural role of fire in particular ecosystems. In those ecosystems which very rarely burn, even a low-intensity surface fire may represent a more intense disturbance than a conflagration in an evergreen shrub bog. Thus, fire intensity from the standpoint of ecosystem response probably cannot be expressed simply as fuel consumed or heat produced. In many cases the lack or reduced frequency of fire results in succession. Past and present fire suppression policies, urbanization, and dissection of the landscape have caused such changes throughout the Southeast. In other ecosystems, reduction in fire frequency seems to result in stagnation and changes within the ecosystem which increase the probability of fire. Fire prevention in such communities is in a real sense a disturbance. It seems unlikely that even the most extensive fire suppression techniques can prevent fires in savannas, pine flatwoods, and shrub bogs. Indeed, suppression may simply result in greater accumulation of fuel and more intense fires when they do occur. Even in vegetation types not normally associated with fire, such as upland deciduous forests, once fire is introduced its effects may be to alter the fuel characteristics, increasing the likelihood of future fire but decreasing its intensity.

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FIRE IN TROPICAL ECOSYSTEMS

Dr. Dieter Mueller-Dombois

Department of Botany
University of Hawaii
Honolulu, Hawaii

ABSTRACT

The review covers fire frequency and distribution in tropical lowland and montane ecosystems. It also draws attention to differences among the major tropical world regions. Fire has been and continues to be particularly destructive in tropical Africa, while high fire frequency in tropical Australia has resulted in a generally more fire-adapted vegetation. Tropical lowland rain forests are essentially nonflammable vegetations, but once invaded by grasslands they become easily degraded by frequent fire. Fire may destroy a good portion of their floristic and ecological vegetation potential. Slash fire following logging increases the fire hazard in tropical forests because it promotes the establishment of pyrophytic grasses. There is, therefore, a significantly different outcome in the use of fire as a management tool in tropical as compared to temperate forests.

KEYWORDS: fire, tropical forests, savannas, succession, degradation.

INTRODUCTION

Scope and Background

This paper attempts to review in form of a comprehensive synthesis the distribution and role of fire in the natural and seminatural ecosystems of the tropics. Of particular interest in this context are the variations of fire occurrence in terms of intensity and frequency in relation to the latitudinal and altitudinal distribution of tropical ecosystems. A concomitant objective is to address the variations in tropical ecosystem development in relation to fire.

Similar reviews on this subject have already been presented, but their scope differs somewhat from the one addressed in this paper. Bartlett (1955, 1957, 1961) compiled a very useful three-volume annotated bibliography. His emphasis was more on fire in relation to agricultural systems and management or mismanagement and less

on fire as an evolutionary stress factor in natural and seminatural systems, a viewpoint taken in this paper. Moreover, Bartlett did not provide a comprehensive synthesis. Comprehensive reviews, however, were given by Phillips (1965, 1968, 1974) for tropical Africa and by Budowski (1966) for the tropical American lowlands. Batchelder and Hirt (1966) and Batchelder (1967) did a pantropical synthesis as is attempted in this paper. Their emphasis, however, was more on a detailed analysis of current spatial and seasonal patterns of fire in individual tropical countries, whereas in this paper the evolutionary and manmade contributions of fire are stressed in relation to tropical ecosystem distribution and development.

The subject matter, in contrast to the preceding U.S. regional papers, spans an area of very much greater size. The tropics, as defined for this paper, include the global belt extending around the Equator north to the Tropic of Cancer and south to the Tropic of Capricorn. The area is not only of very much greater size than the individual U.S. regions treated before, it is also a multinational region which, moreover, is of much greater ecological complexity. However, this paper is not a review of all the available literature on fire in the tropics, and it does not treat effects of fire on soils or plants in any specific detail or the use of fire as a management tool. Although the paper claims to be ecosystem oriented, it ignores any detailed consideration of biota other than plants, grazing animals, and decomposers. A more detailed consideration would go much beyond the scope of this review.

Three basic questions are addressed in this paper:

1. What is the contribution of frequency and intensity of fire to the spatial gradients of tropical ecosystems, i.e., latitudinally in the lowland areas and altitudinally?
2. What are the vegetation and floristic potentials, and the successional and retrogression trends in the tropics in the presence of fire?
3. What, if any, is the difference between tropical and temperate ecosystems in relation to fire?

Fire as an Ecosystem Function

The immediate effects of a fire are fundamentally similar in all ecosystems. They include a more or less radical reduction or consumption of all or part of the vegetation cover and instant mineralization of organic matter. In some cases, particularly in wooded vegetations, a certain proportion of fire-killed wood may not be mineralized but instead be taken out of circulation by charcoal formation. The mineral soil does not burn, but its capacity to support plant growth may be more or less strongly affected in a positive or negative sense. Negative effects occur when the resulting ash is not immediately utilized by plant growth after the fire. Rainfall and the topography of the burned habitat may interact after a fire to remove the ash and thus reduce the site potential.

A critical factor is the survival and regrowth capacity of the vegetation after a fire. Apart from the intensity or severity of the fire, vegetation survival and regrowth is largely related to the question of whether or not fire has been important as an evolutionary stress factor in the development of the natural ecosystems of a region.

This question has been answered positively for nearly all temperate forest ecosystems investigated (Kozlowski and Ahlgren 1974), although there are important differences in fire frequency between regions. A positive answer cannot be given so unconditionally for tropical forests, and tropical rain forests in particular seem to be a real exception insofar as natural fires have played no significant role in their development.

Causative Relationships in Fire Occurrence

The vegetation characteristics themselves are a major determinant of fire occurrence. Fuel-loading capacity in terms of plant density and plant life-form combination (i.e., woody plants of various sizes and herbaceous plants, particularly grasses) determines the fire potential of a vegetation.

The soil substrate and its microorganism activity contribute to the fuel-loading capacity. If decomposition of the annually produced litter is slow, organic matter builds up at the soil surface. This is a major reason for forest fires in temperate environments.

Climate is an overriding control factor in fire occurrence and frequency, since climate determines not only the vegetation characteristics in a general sense, but also influences soil microorganism activity and thus litter decomposition. In tropical lowland environments, litter decomposition is generally fast so that organic matter accumulation is rarely an important factor. However, climatic seasonality in terms of wetness and dryness is a most important parameter related to fire occurrence. Thus, a climate and vegetation analysis is imperative for an assessment of fire occurrence and frequency. Climatic seasonality does not manifest itself only on a month-to-month basis, but also in year-to-year variation.

Moreover, the major natural ignition source for wildland fires--lightning--is a factor of climate. Its importance as the major natural ignition source, however, requires special consideration.

A further determinant in the causal chain, besides man, is the grazing animals or herbivores, particularly in the tropics. Their function as consumers may be so dominant in some ecosystems as to prevent the occurrence of fires in otherwise typical fire regions.

ECOSYSTEM DISTRIBUTION AND FIRE IN THE TROPICS

A Latitudinal Perspective

TROPICAL CLIMATES AND ZONAL VEGETATION TYPES

Climate may be considered the first determinant of fire occurrence, if one can assume ignition frequency (natural and man-induced) to be equal in different tropical regions of the world. Climate is also considered the first determinant of the character of the vegetation, which in turn strongly influences fire frequency and intensity.

Within the global belt of the tropics (from 23° N. to 23° S.) one can recognize three types of tropical lowland climate, the humid tropics, the subhumid or semidry tropics, and the dry tropics. These zones are shown on the world climate map (No. 9) of Walter and others (1975). This map is here reproduced on figures 1 (North and Central America), 2 (South America), 3 (Africa), 4 (Asia), and 5 (Australia). The tropical climate zones (I, I-II, and II) are based on mean monthly rainfall and temperature distribution as defined through a large number of climatic station records. These records are plotted in form of climate diagrams on several 1:8 million scale maps, one for each continent or major world region. A thorough discussion is given in the above publication. Here it may suffice to say that the three climatic zones (I, I-II, II) correspond approximately to the potential terrain of three zonal forest types, the tropical rain forest (zone I extending to approximately 10° N. and S. of the equator in tropical America, Africa, and southeast Asia), the semideciduous forest (zone I-II, recognized as a broad climatic ecotone in tropical America and Africa (but almost absent in southeast Asia), and the dry deciduous forest (zone II, which is the largest tropical climate type as seen by comparing all five maps). Both the latter types occur in



Figure 2.--South America with all climatic zones, except VIII (boreal zone).

Legend continued from figure 1:

- V Warm-temperate climate
- IV Mediterranean climate
- III Subtropical desert climate
- II Tropical seasonal climate
- I Tropical rain forest climate

Note several important transition climates
 I-II Tropical subhumid or transition zone
 I-(rIII) Tropical semidesert, northeastern Brazil.



Figure 3.--Africa with climatic zones I to V. Note large area of tropical subhumid or transition climate (zone I-II) bordering tropical rain forest climate to north, south and east of tropical rain forest climate (zone I). Zones I-III and III (tI) semidesert climates in eastern Africa.

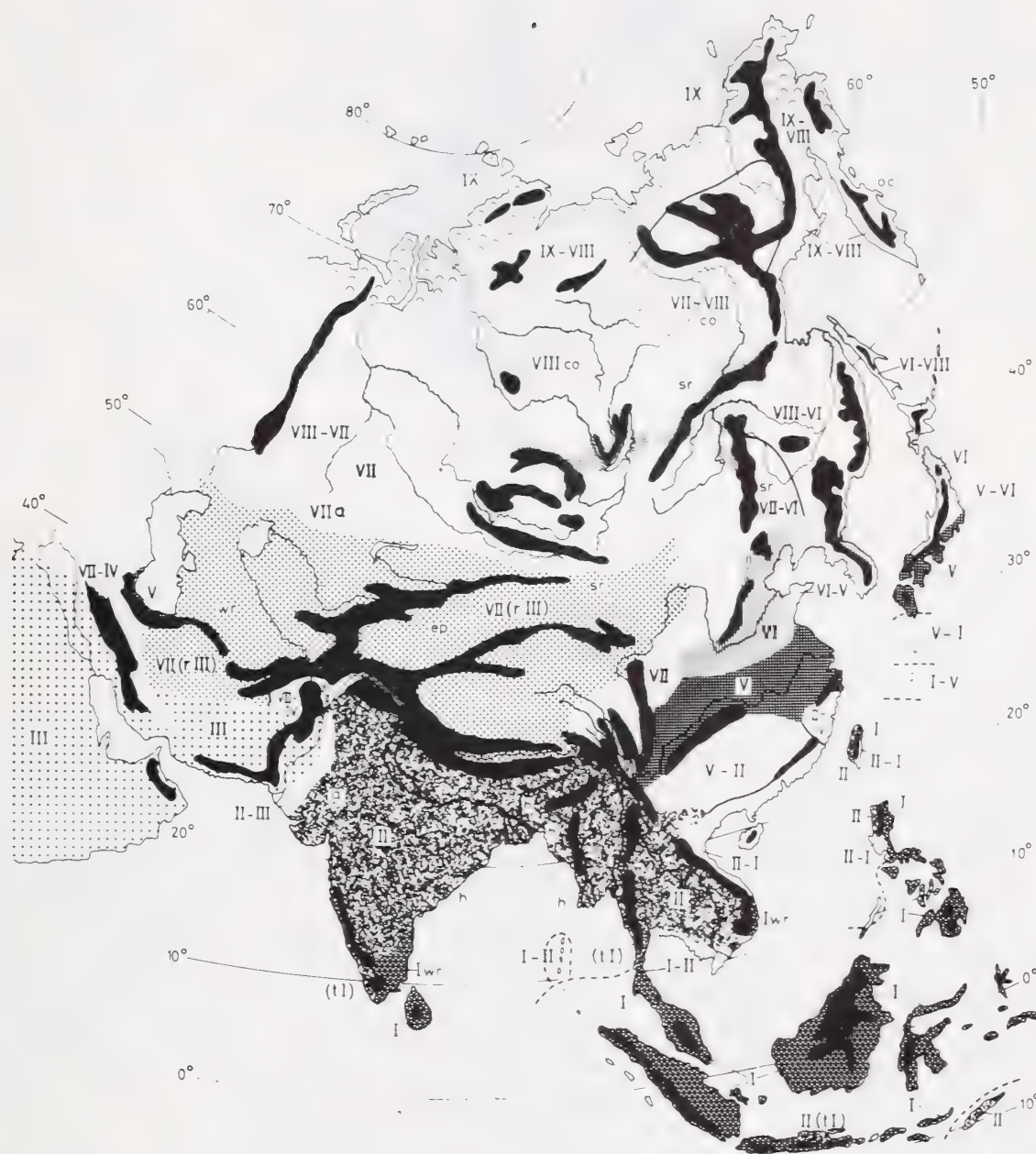


Figure 4.--Asia with climatic zones I to IX.

- I Tropical rain forest climate mostly in Philippines, Borneo, Java, Sumatra, Malay Peninsular and South India
- II Tropical seasonal (monsoon) climate mostly in India, Burma, Thailand, Vietnam (a = particularly dry in northwest India).

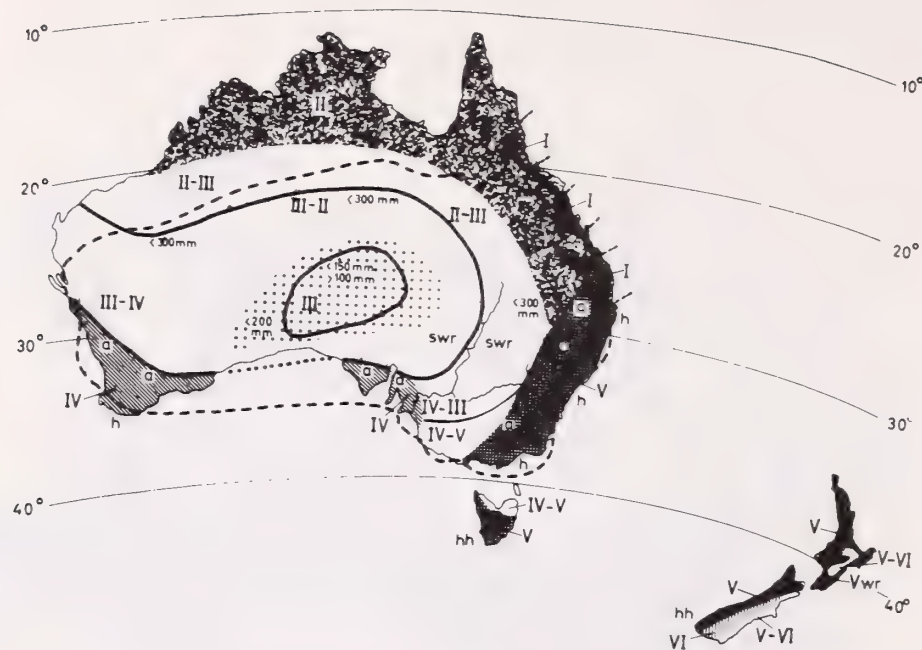


Figure 5.--Australia and New Zealand with climatic zones I to IV.

Legend

- I Tropical rain forest climate
- II Tropical seasonal climate (covers most of Australian tropics)
- III Subtropical desert climate
- IV Mediterranean climate
- V Warm-temperate climate
- Black areas refer to mountain climate
(For further explanation see Walter and others 1975)

seasonal climates, which are characterized by summer-wet and winter-dry seasons. Their differentiation is based primarily on the length and severity of the dry season. In terms of severity, a dry season is recognized as a "drought" season when the rainfall curve undercuts the temperate curve in the climate diagrams. For the purpose of indicating a drought season (wherever applicable) mean monthly temperature and rainfall curves are plotted at the ratio of 10°C to 20 mm in each climate diagram. The rationale for this approach has been presented in Walter and others (1975). A "dry" season is recognized whenever the monthly rainfall is less than 100 mm. The ecotone zone I-II includes stations with "dry" seasons and short "drought" seasons of usually less than 2 months duration, such as found, for example, in the lower Amazon Basin at Manaus. The zone of the dry-deciduous forest is characterized by longer "drought" seasons varying throughout zone II from 2 to 8 months. Further within zonal variations are indicated, such as for northwest India, where zone II is particularly arid (see symbol "a" meaning particularly arid for zone II, fig. 4).

In addition it should be mentioned that tropical Asia and Australia lie in the monsoon climate, which here refers particularly to the seasonal climate of zone II

in India, Indochina, and Northern Australia. This area supports mostly a mixed deciduous forest (a term referring to evergreen sclerophyll and deciduous trees growing in differing combinations) or an evergreen sclerophyll forest. The latter occurs in tropical areas with an approximate reversal of seasonality, i.e., summer drought and autumn-to-winter wetness. Such an area occurs in the dry zone of Sri Lanka and southeast India and also, for example, on the leeward side of the Hawaiian Islands, which, however, lie in the tradewind belt. This climate compares to a Mediterranean rainfall seasonality. The month-to-month temperature, however, follows typically a tropical trend, i.e., there is relatively little temperature difference between summer and winter.

A fourth tropical climate type should be mentioned, the tropical arid or equatorial semidesert climate. This is restricted to relatively small areas on the eastern extremities of tropical America and Africa (zones I-III on figs. 2 and 3). These arid areas are potentially occupied by strongly xerophytic woodland, or thorn-scrub with succulents. They include the Caatinga of northeast Brazil (Huek 1966) and a scrub-succulent desert in Eastern Africa (Walter 1971).

TROPICAL SAVANNAS AND OTHER VEGETATION TYPES

Tropical savannas and grasslands, which form a very large proportion of the semi-natural and natural vegetation in all major tropical regions of the world, were not mentioned among the five major zonal vegetation types. Savannas, which can be defined morphologically as vegetation types of scattered trees and/or shrubs, growing in a matrix of more or less closed herbaceous vegetation covers (usually composed dominantly of grasses), are no longer considered to be climatic climax or zonal vegetation types. This treatment is by no means obvious, but agrees with most authors who have given serious thought and study to the problem of the dominant control factors in savanna development (Aubreville 1949, cited in Bartlett 1955, Richards 1952, Whyte 1968, Walter 1971, and Sarmiento and Monasterio 1975). However, Walter (1971) presents evidence that there is a grassland and savanna climate in the subtropical lowland area of southern Africa. A brief discussion of viewpoints relating to the origin of tropical savannas will be given in the section under "Vegetation Potential and Fire." Here it will merely be pointed out that tropical savannas occur in four of the five tropical vegetation zones, generally as a smaller subcomponent in the humid tropical rain forest zone, and as the dominant vegetation components in the three seasonal climates, the subhumid or semidry transition area (I-II), the summer-wet and winter-arid or -dry tropics (zone II), and the tropical monsoon and seasonal tradewind climates (zones II and II-IV). Closed grass-cover savannas are apparently rare in the tropical arid or semidesert climates (zone I-III). Savannas are today the most widespread tropical vegetation types and with few exceptions (e.g., the Aripo savanna in Trinidad, Beard 1946), they are considered the tropical fire-type vegetation. This does not mean, however, that all savannas are believed to have originated from natural fires. It merely means that all authors consulted agree on the point that the tropical savannas are maintained today by frequent man-caused fires. This is not surprising, since closed grass and sedge covers, even where occurring in year-round humid climates or on year-round water-soaked soils (i.e., marshlands) have been found to burn periodically.

It is well known that zonal tropical rain forests occur typically on well-drained, deeply weathered lateritic clay soil (oxisols and ultisols), which contain very little organic matter and nutrients. These soils are very acidic (generally pH 4.2-5.6) and contain poor oxide clays with very low exchange capacities. They commonly display the property of irreversible drying when exposed to strong desiccation at the

Whitmore (1975) described several other tropical lowland rain forests which occur on quite different soils. There are the tropical heath (Karangas) forests on podzolized sands; the rain forests on limestone, on ultrabasic (serpentine) rock, and on calcareous

sand and coral rocks along beaches, and the peat-swamp forests. All are significant edaphic variants, which can be treated as intrazonal forest types in the tropical rain forest terrain.

Heath forests are relatively low-stature forests or woodlands consisting of evergreen sclerophyllous species, many of them belonging to the family Myrtaceae (Whitmore 1975). Trees also include some conifers such as Dacrydium and Podocarpus species. Casuarina is a common associate. The creeping or mat-forming Dicranopteris fern, clubmosses (Lycopodium spp.), and certain graminoids (Gahnia, Cladium, and Dianella) occur occasionally as undergrowth in more open places. There is some, although usually thin, organic overlay on the mineral soil. The forest on podzol (or spodosol) is easily degraded by burning to an open savanna or low scrub called "padang" in Sarawak (southeast Asia). There are also heath forests widely distributed throughout the Amazon Basin and in the Guianas (Hueck 1966). The African rain forest contains only a small area in Gabon. (A recent study of this forest by McKey and others [1978] points to the high content of phenolics in the leaf tissues of many of its tree species.) These heath forests are known to be susceptible to fire under certain conditions (Whitmore 1975). The same applies to rain forests on limestone and serpentine soils. In southeast Asia the paperbark tree (Melaleuca leucadendra) and the ironwood tree (Casuarina spp.) are common associates among several other somewhat xerophytic evergreen tree species of the Myrtaceae (e.g., Tristania obovata) and conifers (Dacrydium beccarii, Phyllocladus hypophyllus). Ericaceous shrubs are found in the understory, such as Rhododendron and Vaccinium species and Styphelia, a member of the Australian heath family Epacridaceae.

Limestone substrates are excessively drained and serpentine soils contain phytotoxic elements (Ni, Co, Cr). Therefore, microorganism activity is impeded and there is a certain amount of raw humus accumulation on the forest floor. Fire from lightning has been reported in the limestone forest on Gunning Api in Sarawak according to Whitmore (1975). ("Api" means lightning in Malaysian.) Inland limestone forests are found also in tropical America, for example on Cuba (Knapp 1965, Walter 1971). Serpentine forests seem to be rather rare in general.

Coastal limestone forests have similarly low microorganismic activity and when stocked with Casuarina, raw humus accumulates. Such forests can undoubtedly have natural fires, even in the humid tropics.

Peat-swamp forests are an important rain forest type in southeast Asia (Whitmore 1975), also in tropical America (Hueck 1966) and Africa (Knapp 1973). In spite of their often turflike accumulation of organic matter, natural fires have apparently not been observed in this edaphic variant of the tropical rain forest.

Similar edaphic variations occur also in the tropical seasonal environments. Here, excessively drained sites (such as limestone soils) are, of course, even drier, and poorly drained soils begin to reflect the climatic seasonality. There are large stretches of savanna in tropical America, e.g., in the Venezuelan Llanos, but also in Africa where the surface is inundated during the rainy season and where the same substrate is bone dry during the dry season. It is generally agreed (Richards 1952; Walter 1971, 1973; Heck 1966; Knapp 1973; Sarmiento and Monasterio 1974) that these alternately wet and dry soils support a natural or primary savanna, and that fire is only an accessory factor, which does little to change the general spatial relationships of the more or less closed grass cover and the scattered trees. In the more heavily inundated portions of this primarily edaphically controlled savanna, palms (Copernicia in South America and Borassus in Africa) are the only tree life forms that can coexist with the grasses and sedges (Beard 1953). In addition, these palms are very fire resistant. Sarmiento and Monasterio (1974), in their excellent review of the savanna-origin problem, described this edaphically controlled savanna as "hyperseasonal," to point out that it is not only the soil but also the climate which is responsible

for the formation of this important tropical vegetation type. The soil properties accentuate the strong climatic seasonality. The soil becomes almost cemented during the dry season. This seasonal soil moisture regime contrasts strongly with that of normally drained soils. Yet, one can certainly not speak of a grassland or savanna climate as has often been done.

Table 1 gives a brief summary of the relationships discussed.

TABLE 1.--Generalized spatial gradient of tropical ecosystems

Climatic zones (symbols as on maps)			
I	I-II	II	I-III
<u>Zonal Ecosystems Gradient (wet to dry)</u>			
Rain forest	Semi-dec. forest (Monsoon forest)	Dry dec. forest	Desert scrub & succulents
<u>Intrazonal Ecosystems</u>			
Heath forest			
Forest on limestone	"Hyperseasonal" savannas		} Very sparse desert grass Important edaphic variants
Peat-swamp forest			
Tall-grass savannas		Mid-grass and short-grass savannas	} other variants*

*Mostly anthropogenic.

I can now begin to answer one of the basic questions, namely: What is the contribution of fire to the spatial gradient of tropical ecosystems? Table 1 indirectly indicates fire as a dominant factor for the savannas listed at the bottom of the table. These are characterized as mostly of anthropogenic origin. Shifting agriculture and grazing have acted as concomitant causes together with fire in the development of these savannas, which include pure grasslands. As shown on table 1, they range throughout the tropical territory of the wettest rain forests to the driest dry-deciduous forests.

Man-caused savanna and grassland fires are an extremely important and frequent ecological phenomenon throughout most of the tropics today (Bartlett 1955, 1957, 1961; Phillips 1965, 1968, 1974; Budowski 1966). But what about natural fires? These are of much greater ecological significance, when we are concerned about fire adaptation of ecosystems and species.

Lightning is considered one of the most important natural causes of fire in vegetation. Komarek (1964) analyzed the distribution of lightning storms over the surface of our planet. His map shows that there are many more thunderstorms per year in tropical America than in temperate America. Up to 200 thunderstorm days are recorded for the Amazon area versus 60 to 80 for the southeastern U.S. (Florida) and 5 to 10 for the Pacific Northwest and the Boreal forest. Similarly, for equatorial Africa there are 100 thunderstorm days recorded per year (which is high) and for southeast Asia the frequency shown is 140 for the Malay Peninsula, 60 for Sarawak on Borneo, and about 40 for northern Queensland and New Guinea. Thunderstorms and thus, lightnings, are clearly most frequent in the humid tropics. Yet, I could find no reference to lightning-caused fires anywhere for the zonal tropical rain forest on latosols. Whitmore (1975) states that "primary rain forest within the principal ever-wet parts of the Far East appears to be mainly noninflammable." Budowski (1966) refers to fires which were observed on isolated mountain peaks in southern Venezuela, where there was no human encroachment. However, he does not specify whether the natural vegetation there was tropical rain forest. If it was rain forest, then it could have been montane rain forest (which usually shows some accumulation of organic matter on the soil surface) or it could have been one of those edaphic variants (such as limestone forest or heath forest) that have been known to burn from lightning (Whitmore 1975).

Thus, lightning fire can occur in the lowland tropical rain forest, but only in those edaphic variants where some raw humus accumulates. Certainly, even in these edaphic variants, lightning fire must be very rare, because lightning is usually associated with heavy rainstorms in the humid rain forest terrain.

It is interesting, however, that lightning plays an important role in some lowland tropical rain forests as a perturbation factor. Lightning damage causes local successions and stand rejuvenation, for example, in dipterocarp peat-swamp forest of Sarawak (Brünig 1964, Anderson 1964). Brünig found gap sizes caused by lightning to range from 400 m^2 to over $8\,000 \text{ m}^2$ and the average gap size was $2\,000 \text{ m}^2$. He also points out that wind damage tends to enlarge the lightning gaps in many places. Anderson (1964) reported that 70 trees may be killed in this peat-swamp forest by a single electric charge. The damage seems to manifest itself merely in a sudden death of trees with some breakage but without much scorching and no fire occurrence. Anderson studied other areas of lowland dipterocarp forest and concluded that incidence of lightning damage depends on four factors: the structure of the canopy (even-canopy forests show larger lightning gaps than uneven-canopy forests with emergents), topography (more lightning damage in flat terrain), species (some, e.g., *Shorea albida*, are more susceptible than others), and lightning frequency. He also suspects that high water tables are related to frequency of lightning damage since he found most of the damage in peat-swamp and mangrove forests.

Lightning may be a natural cause of forest fires in the other two zonal forest ecosystems of the tropics, the semideciduous and dry deciduous forest. There is a distinct and, in the second case, a severe and prolonged dry season that provides for excellent fire conditions. However, one should also ask the question of what is there to burn? Both types of forest do not accumulate much humus on the surface. Termites are very active and break down even small branches in relatively short time. The semideciduous forest does not even provide much in the way of a continuous litter layer from the current year's leaf drop. This is different with the dry-deciduous forest, which contributes a large amount of litter to the surface each year. In India, foresters distinguished between two general classes of forest, the deciduous forest, which unless protected is burned (through man-caused fires) every year and the green (monsoon sclerophyll) forest into which as a rule fire does not enter (Brandis 1906, see Bartlett 1955). The relationship is certainly one of fuel loading near the ground. Where the dry-deciduous forest has a closed canopy during the wet season, it is practically barren or with only sparse undergrowth during the drought season. Unless such forest floors are covered with a continuous layer of leaf litter during the dry season, they do not burn easily.

The situation changes in the so-called savanna woodlands, which are somewhat more open low-stature forests with an undergrowth of grasses. Here fire penetrates readily depending on whether the grassy undergrowth is continuous or discontinuous. Richards (1952) says of these savanna woodlands that they may be a climatic climax; that is, a primarily climatically controlled, but more open, form of the dry-deciduous forest. This is a difficult question to resolve. It is also possible that such forests resulted under natural conditions from herbivore interaction in combination with fire.

It is clear, however, that the seasonal tropics supports areas of natural, primarily edaphically controlled savanna and grassland, as typified by the "hyper-seasonal" savanna on table 1. It can be assumed that fire has been part of the natural savannas from time immemorial, before man came on the scene. Lightning is known to have started fires in grassland (Daubenmire 1968a, Vogl 1969, 1974). It is also possible that self-combustion may be a natural cause of fire. This has been proven for marshes in Louisiana (Viosca 1931) and could very well apply also to tropical savannas. Other natural fire sources, such as falling stones in mountainous terrains (of southern african grasslands) or translucent stones (Knapp 1973) may be mentioned, but lightning alone would probably be sufficient to explain fire as a stress factor, which has occurred at a certain frequency during evolutionary time.

This means that one can expect species and ecosystem adaptations to fire in these savanna ecosystems. However, it does not mean that they have a fire origin. In contrast, in the zonal tropical forest ecosystems, one can expect far less adaptation to fire than in temperate forest ecosystems. Fire is also of little or no importance in the thorn scrub and succulent vegetation of the equatorial semideserts (Walter 1971), primarily because of the sparseness of the vegetation cover.

Variations Among Tropical Regions

We have seen that fire occurrence is only conditionally related to lightning frequency. In spite of receiving the highest frequency of lightning discharges in the world, natural fires in the humid tropics are the exception rather than the rule. The overriding factors are rainfall seasonality and the characteristics of the vegetation. Fire may begin its importance as a natural factor in the transition zone (I-II), while it undoubtedly had a significant evolutionary impact on the strongly seasonal tropical desert zone.

Because of the existence of vast areas of natural (primary) savanna, the tropical seasonal zone (in tropical Africa and America) can be regarded as one of the world's ancient fire-stress environments. However, the zonal forest vegetation here may be less adapted, because the fires have occurred primarily in the grasslands and savannas and less in the zonal forests. Budowski (1966) emphasized that tropical fires are mostly grass fires.

In Africa, fire may have more readily penetrated from savannas into adjoining dry-deciduous forests on account of the abundance of large herds of grazers and browsers. Particularly the elephant, with its requirement for frequent alternation in its diet of herbaceous and woody plants (Eisenberg and Lockhart 1972, Mueller-Dombois 1972), may have created openings in the dry forest. These may have been invaded by grasses as seral species, a process which is also going on today (Buechner and Dawkins 1961, Laws 1970), but under somewhat different circumstances with the aid of man.

A sudden and significant increase in the frequency of fire must have occurred when man began to use fire as a tool for hunting, tribal warfare, and agriculture (i.e., for renewing pastures and for land clearing). According to Knapp (1973), man-caused fires appeared historically later in Africa than in Europe, i.e., in the late stone age. However, fire has been applied more drastically by man in Africa than in any other tropical world region (Richards 1952, Hedberg and Hedberg 1968). The most destructive influence of man's use of fire in reducing tropical forests in Africa as compared to tropical America becomes apparent also from the differing emphases in the regional fire reviews of Phillips (1965, 1968, 1974) and Budowski (1966). Budowski emphasizes grass fires and points out that these, and not forest fires, are the important tropical vegetation fires. Phillips emphasizes the destructiveness of fires in tropical forests and points out that the forests in tropical Africa have receded drastically on account of fire. The same message of greater forest destruction due to man's use of fire in Africa comes through Knapp's (1965, 1973) books dealing individually with both tropical regions.

The two kinds of fire influences are not necessarily mutually exclusive in the ecological sense. Phillips (1974) admits that it is often difficult to separate the influence of fire on forest destruction from that of shifting agriculture and grazing. In other words, fire may significantly penetrate and become destructive in tropical forests only after openings are created and they have become invaded by grasses. Relatively large openings are certainly created by shifting agriculture and subsequent abandonment, but forest openings can also be created naturally by elephants, for example, or by lightning and storms. The latter are effective also in other tropical regions.

An interesting regional comparison may be drawn from a look at the gallery forest environment. Gallery forests are considered edaphically controlled outliers of the tropical rain forest (Richards 1976). Knapp (1973) describes them in Africa as being typically surrounded by grassland or savanna. The sharply bordering grasslands or savannas are believed to have been derived from repeated fires, which stopped at the gallery forest. A similar pattern is shown on Hueck and Seibert's (1972) map of South America, on which gallery forests extend into savanna and grasslands north and south from the Amazonian rain forest. Whitmore (1975), in contrast, describes for southeast Asia (Thailand-Burma) monsoon forests as the typical bordering vegetation of evergreen gallery forests.

Perhaps this is not really so significant because there are, of course, also variations from place to place within each major tropical region and these may have had differing histories with regard to fire as an evolutionary stress factor.

However, Richards (1976) also says that there is in southeast Asia a relative scarcity of grasslands and open savannas as compared to tropical Africa and America in comparable climates.

MOUNTAIN VERSUS LOWLAND TROPICS

Comparisons are often made between tropical upland (montane environments) or mountain environments and the temperate lowland environments at higher or lower latitudes. There is validity in this for certain purposes. With regard to fire relationships there are two conditions which are quite similar.

First, there are often floristic similarities at higher taxonomic levels. In the mountains of tropical Mexico, for example, one encounters forests with oaks and pines (Knapp 1965). The same is true for southeast Asia (Whitmore 1975). In the mountains of tropical Asia occur certain conifers which also have lowland distributions in temperate latitudes of the southern hemisphere, such as Araucaria and Podocarpus. The undergrowth often contains Ericaceae, such as Rhododendron and Vaccinium species, which also form mountain scrub formations above timberline (Troll 1959). These are more xeromorphic genera, and one can expect better resistance to fire among their species than among many of the humid tropical lowland taxa. An important floristic affinity also exists among the grasses, which often contain temperate zone genera such as Deschampsia, Agrostis, and Trisetum (Mueller-Dombois 1967).

Second, as one goes up under forests in tropical mountains, organic matter begins to accumulate on the ground, and there is generally a substantial humus layer, sometimes of raw humus, on the forest floor similar to that found in temperate forests at higher latitudes.

However, the temperature, light, and rainfall seasonality in tropical mountains is very similar to that of the tropical lowlands. The month-to-month temperature varies little. In other words, there are no cold winters or hot summers. The only important temperature difference to the tropical lowland climate is that the entire month-to-month temperature curve responds to the lapse rate (i.e., about 0.5° - 0.6° C decrease per 100 m increase in altitude) and to the local inversion phenomena. Day length varies little between summer and winter as in the corresponding tropical lowlands. The rainfall seasonality of the lowlands is also reflected in the mountains although here orographic effects bring about important variations. Such variations are, for example, very important the Hawaiian Islands with rain forests on the windward sides of the mountains and strongly seasonal forests (with winter rainfall and pronounced summer drought) on the leeward sides. This windward-leeward pattern occurs everywhere in the tropical tradewind zone, for example; also in tropical America (Alisio forest, Hueck 1966), in the Caribbean Islands (Beard 1949), and in the monsoon climate of south Asia (Mueller-Dombois 1968).

Since tropical mountain climates correspond in these significant attributes to their corresponding lowland climates, it is not advisable to refer to them as subtropical or temperate climates. Instead they are better referred to as cool tropical or tropical mountain climates.

The landscapes of Sri Lanka and Hawaii both contain lowland and mountain ecosystems. Since the writer had an opportunity to do ecological research in all these ecosystems, they may here serve as case examples for comparing fire distribution along altitudinal gradients.

ALTITUDINAL VARIATION OF FIRE IN SRI LANKA

Ceylon (now Sri Lanka) is mentioned by Richards (1976) as an exception in the Asian tropics insofar as the country contains large areas of monsoon grassland and savanna. Grass fires, therefore, should be an important ecological factor in Sri Lanka,

and indeed much study and thought has been given to the role of fire and the origin of these grasslands and savannas (Pearson 1899; de Rosayro 1945, 1946; Holmes 1951; Perera 1967, 1969; Mueller-Dombois and Perera 1971).

The Monsoon Grasslands

Holmes (1951) distinguished four general types of monsoon grassland and savannas in Sri Lanka, named locally "talawa," "damana," "villu," and "patana."

The talawa grasslands are anthropogenic grasslands in the humid lowlands which originated from shifting agriculture in the rain forest. They are maintained by frequent fires and include the "kekilla" fernlands, which are covered with Dicranopteris (= Gleichenia) linearis, a mat-forming creeping heliophytic fern, which is also indigenous to the Hawaiian Islands.

The damana and villu grasslands are also lowland ecosystems but they occur in the (seasonally) dry zone of Sri Lanka. This dry zone extends over about three-quarters of the island in the north, east, and southeast. Damana grasslands and savannas are those occurring on dryland or well-drained soils, and villu grasslands occur on more or less permanently water-soaked soils. The damana grasslands and savannas are in most cases the end stages (or fire climaxes) of former "chena" land, i.e., land that has been cultivated and abandoned (shifting cultivation). The villu grasslands are usually found around the many "water tanks" of the dry zone. These water tanks are not cement basins, but mostly artificial lakes or fresh-water swamps; many of them were built over 2,000 years ago. They were constructed and are maintained through diking of stream water. There are many streams and tributaries that flow from the wet-zone highland and mountain areas in the southwest of Sri Lanka into north, east, and southeast directions through the dry zone. The tanks are placed strategically throughout this zone. The tank water is used in most cases for rice irrigation during the dry season. A severe drought occurs in the dry zone during the time of the southwest monsoon. This season lasts from early June through mid-September, when the southwest monsoon brings rain to the southwest quarter of the island, where the mountainous area is located. During the southwest monsoon the dry zone is under the leeward desiccation effect, which is further heightened by the "kachan," a hot, drying wind which blows most of the time with considerable speed. During this season, man-caused fires occur in many of the lowlands. Even the wet villu grasslands are frequently burned. With the oncoming of the northeast monsoon in early fall (late September or early October), the dry zone becomes a "wet zone." The northeast monsoon rains coincide with the fall conventional rains. The latter are common to all humid areas in the equatorial belt (10° N. and 10° S.). The northeast monsoon rains decrease usually by mid-December and cease in January. Following the northeast monsoon, a short dry season occurs in February, which extends over both the dry and wet zones of Sri Lanka. At that time, fires occur in the talawa grasslands of the lowland wet zone. These are deliberately set, often by children for excitement and fun. Kekilla fernlands are burned occasionally for getting rid of snakes (Holmes 1951). The fire season stops with the onset of the spring conventional rains, which occur through April and May. Thereafter, the southwest monsoon begins again.

The patana grasslands and savannas are montane grasslands, which range from 490 m elevation to the highest peneplain (Horton Plains) at about 2 295 m. They are recognized generally as "dry" and "wet" patanas. The dry patanas occur in the middle elevation range from 490 m to 1 639 m, and the wet patanas in the upper range from 1 639 m to 2 295 m.

The dry patanas are called "dry" because they occur on very permeable red and yellow latosols. However, there are two distinct climatic components of dry patana; one occurs in the wet rain forest zone of the Western Basin, the other in the summer-dry (seasonal) zone of the Uva Basin.

A vigorous argument arose about the origin of the Uva Basin dry patana among two of Sri Lanka's foremost ecologists. De Rosayro (1945, 1946) believed this grassland to represent a climatic climax, while Holmes (1951) argued for a fire climax. The mean annual rainfall of the Uva Basin varies from about 1 400 mm to 1 800 mm, and there is no question that this is a forest climate. There is also no real evidence for de Rosayro's argument that the Uva Basin dry patana developed from swampy conditions during an earlier wetter climatic period.

However, some grassland may have originated naturally before man began to use fire. Sri Lanka has a rich natural community of large herbivores including elephants. These no longer range into the Uva Basin, but were formerly recorded to be all over the island even in the rain forest. It is quite conceivable that elephant activity has not allowed formation of closed forest in the Uva Basin so that there was a natural niche for graminoid life forms. Even though a montane tropical climate with this amount of rainfall favors a closed mesophytic forest, the natural vegetation of the Uva Basin may have been a savanna woodland or even a parkland formation. Natural fires occurring at low frequency probably influenced this vegetation before man changed it to pure grassland through the use of frequent fires.

The present landscape of the Uva Basin consists of rolling grass-covered hills and depressions filled with scrub or small groves of trees, or in the wetter spots with sedge swamps. The grass cover on the hills shows patches of bunchgrass in a matrix of short-grass cover. The bunchgrass patches, mostly formed from Cymbopogon nardus, are burned very frequently, often twice per year, once during the longer summer-dry season and often a second time during the short dry season in February. The short-grass cover matrix is kept short as the result of constant grazing by cattle. It is composed primarily of creeping or mat-forming (rhizomatous and stoloniferous) grasses such as Chrysopogon aciculatus, Digitaria longiflora, Brachiaria distachya, and others. Fire does not, as a rule, penetrate from the bunchgrass patches into the short-grass matrix, because of the absence of combustible fuel in the latter. There is a dynamic relationship between the two grass cover types. Very frequent burning reduces the size of the bunchgrass patches. Less frequent burning (i.e., once every year or two) maintains them. Still less frequent burning allows establishment of shrub species. Overgrazing of the short-grass cover promotes establishment of the less palatable bunchgrasses in the short-grass cover, where they then form new patches.

The soil on the grasslands knolls and slopes is truncated from erosion, probably the result of frequent burning combined with flash floods (Joachim and Kandiah 1942). An A horizon is usually lacking (Mueller-Dombois and Perera 1971).

The dry patana in the rain forest zone is typically a closed tall-grass cover. Its dominant species is also Cymbopogon nardus. Imperata cylindrica and Themeda tremula are common associates. This humid-zone dry patana, which occurs mostly in small areas between tea plantations, is burned annually in most places during the short dry season in February. It is most productive and vigorous during the rainy period of the southwest monsoon in the summer, when the Uva Basin dry patana burns in many places for the second time, because the latter is then exposed to the leeward desiccation effect.

The wet patana, which replaces the dry patana upslope in the humid zone at about 1 640 m, occurs on black soils and is thus also known as "black" wet patana. Going upslope, the soils under grass turn very suddenly dark at about 1 640 m. This elevation corresponds to a mean annual temperature of 18° C. At this temperature, soil micro-organism activity slows down markedly resulting in a substantial accumulation of humic acid colloids and a new equilibrium of organic matter breakdown. The annual rainfall in the wet patana (e.g., Nuwara Eliya 2 154 mm) is not greater than in the dry patana of the humid zone (e.g., Kandy 2 131 mm, Mueller-Dombois 1968). The seasonal variation of rainfall is also the same so that the wet patana also experiences the short dry season in February, when many areas of the wet patana are burned every year.

The black wet patana is well developed at Horton Plains, which is the highest peneplain in Sri Lanka at 2 295 m. Here the grassland occurs on gently rolling hills (similarly as the dry patana in the Uva Basin), but the hilltops are mostly covered with remnants of montane rain forest and the grassland is surrounded also by this forest which forms a sharp boundary with the grassland. The wet patana is rich in endemic species. Two of the more important grasses are Chrysopogon zeylanicum and Arundinella villosa.

This upper montane grassland is apparently also very ancient, but both de Rosayro and Holmes agree that it is of anthropogenic origin. Fires may have been set in the naturally treeless sedge and bamboo (Cheimonobambusa densifolia) swamps (the "deniyas") occurring in the depressional habitats between the rolling hills of Horton Plains. From here the grass cover is believed to have spread over the slopes and knolls, merely from periodic fires without the aid of shifting cultivation (Holmes 1951).

Montane Rain and Lowland Monsoon Forests

The grass fires in the wet patana do not normally spread into the adjacent montane rain forest. They stop sharply at its border, where one usually finds a narrow (1 to 3 m) ecotone consisting of shrubs and ferns (including the bracken fern, Pteridium aquilinum). However, occasionally even this ecotone community burns and a few trees at the forest border are scorched. We observed a group of scorched rain forest trees over a period of 2 years and found that they did not recover. It is conceivable that the rain forest has given way in this manner very slowly to the grassland by losing a few trees at a time to fire. There are apparently very few fire-resistant trees in the montane rain forests of Sri Lanka. A notable exception is Rhododendron zeylanicum, which forms lignotubers (Ekanayake 1962).

This forest displacement with the aid of man-set grassland fires is distinctly different from the more rapid form of displacement with the aid of shifting cultivation as has been practiced in the lowland rain forest of Sri Lanka. Shifting agriculture is still practiced in the monsoon forest, where it has given rise to the formerly discussed damana grassland and savannas.

The monsoon forest in Sri Lanka is primarily an evergreen sclerophyll forest and, although natural fires are expected to have played a role (Whitmore 1975), they must have been and are even today very rare, since even under the high frequency of man-set "chena" fires and villu and damana grassland fires, they do not penetrate readily into the neighboring monsoon forests. This observation was made in Wilpattu National Park (in north Sri Lanka) where several grass fires were witnessed but never a forest fire. Wildlife habitat and vegetation surveys (Mueller-Dombois 1973a) rarely revealed charred trunks or charcoal on the ground. There is no humus on the forest floor and undergrowth is sparse in the closed monsoon forests.

A contrasting situation was found in Ruhuna National Park, southeast Sri Lanka. Here a primarily deciduous thornscrub and open forest vegetation forms the dominant woody plant cover. There are only small areas of closed evergreen sclerophyll forest. The deciduous scrub seems to represent a seral stage or browse-climax, which is arrested in this stage largely on account of elephant feeding (Mueller-Dombois 1972).

The villu and damana grasslands in Ruhuna National Park were rarely found burning in contrast to those of Wilpattu Park. Here the reason was simply animal feeding. Ruhuna Park was so heavily stocked with water buffalo that the grass covers were kept very short to within 10 cm height year-round. Fire, even when started in a less heavily grazed section, never spread very far. Thus, grazing can also be an effective fire control under natural or seminatural conditions.

Many of the woody plant species showed great capacities to withstand mechanical damage from animal feeding by vegetative resprouting. Although we did not observe their response to fire, it would appear that resprouting capacity following animal feeding will also equip these plants to withstand some level of fire activity. Moreover, xeromorphism as expressed by bud formation (which is lacking in tropical rain forest trees) among the deciduous members of the monsoon forest and thick, corky bark, as displayed for example by Manilkara hexandra (a major dominant tree in Ruhuna Park), would likewise equip these woody plants to survive occasional fires. Ground fires, whenever occurring in monsoon forest and deciduous scrub, will rarely be as intense as in temperate-zone forests, because of the absence of any appreciable organic matter layer on the soil surface.

ALTITUDINAL VARIATION OF FIRE IN HAWAII

Hawaii, in contrast to Sri Lanka, is a very isolated part of the world surrounded by vast areas of ocean. Therefore, large browsing animals never became part of the evolutionary stress factors shaping its vegetation. However, fire has been considered a natural stress factor in an important review paper by Vogl (1969). This is an opportunity to reexamine this theory.

Fire in Hawaii's Lowlands

Vogl showed quite convincingly that lightning can be a natural cause of fire in Hawaii as it is elsewhere. The lightning frequency in Hawaii (30 to 50 lightning days/year) corresponds closely with that of the southeastern United States, which is known as a natural fire region (Christensen, this volume).

According to Vogl, lightning-caused fires have occurred in the grassy hills inland (mauka) of Kaneohe of Oahu. However, this is grassland comprised dominantly of broomsedge (Andropogon virginicus), which is only a relatively recent (about 1920, Bryan 1977) introduction to the Hawaiian Islands.

The grass has become established in former rain forest terrain, mostly on abandoned fields (Mueller-Dombois 1973b). Where not maintained by periodic fires, these grasslands were invaded by shrubs and trees. Many now form seral savannas on the windward side of Oahu.

Like other tropical environments, the State of Hawaii does not have a grassland climate. The climate of Hawaii favors woody plant formations in all habitats, except perhaps in the climatic desert environment at the northwest side (Kawaihae) of the island of Hawaii and in the highest mountain areas. However, in both these extreme environments a sparse woody scrub cover may be expected as the potential natural vegetation.

Thus analyzing fire as an evolutionary force in Hawaii, one of the first questions one may ask is: What was there that would have burned from natural causes?

A natural dry-forest remnant with evergreen sclerophyll species of Sapindus, Canthium, and Diospyros occurs still inland at the north shore on Oahu (Hatheway 1952, Wirawan 1974). This forest is virtually self-protected from fire, because of the lack of combustible undergrowth even today, where so many grass species have been introduced. The forest typically also lacks an organic layer at the surface. However, one cannot assume that closed dry sclerophyll forests covered all of the leeward lowlands prior to the arrival of man, about a thousand years ago. On the island of Hawaii there are recent lava flows in this environmental section that could not have supported a closed forest. However, widely scattered woody plants without a grassy matrix to grow in would not be a vegetation conducive to fire either, although undoubtedly many of these trees burned periodically from the heat of passing lava flows. But without a fire-carrying matrix of herbaceous plants, such fires were merely localized, totally consumptive, burns that would leave nothing but charcoal behind.

However, there is one ecologically significant native grass in the dry zone of the Hawaiian Islands. This is Eragrostis variabilis, a tall bunchgrass. It occurs, for example, as a remnant patch of less than 0.2 ha size on southeast Oahu (near Blow-hole). Individual bunches or small patches can be found elsewhere. It is likely that this grass formed a sufficient matrix for carrying natural lightning and perhaps lava-flow fires in the islands during its prehuman vegetation development. Under natural conditions there are many open situations, for example, near the shore, on lava flows and ash deposits, on landslides, or generally during the slow stages of primary succession.

Since E. variabilis is today merely present in small remnant patches, one can assume that it does not thrive under high fire frequency as do some of the later man-introduced grasses, particularly the piligrass, Heteropogon contortus, which is believed to have been brought by the Hawaiians (Fosberg 1972). This grass dominates in some parts of the leeward lowlands next to another important fire-resistant grass, the Natal redtop, Rhynchelytrum repens. There are several other introduced grasses, which do form dry-grass communities on Oahu (Kartawinata and Mueller-Dombois 1972) and other islands (Mueller-Dombois and Spatz 1975). These are maintained either by grazing or periodic fires. Fires are today more or less accidental (for example, the recent Kawainui marshland fire in Kailua, Smith 1977), because there is no use of fire as a management tool in Hawaii other than for sugarcane burning. However, in the past, the Hawaiians apparently used fire in the lowlands to maintain the Heteropogon grass cover (see Vogl 1969).

Grasses are not the only plant life form that carry fire readily when growing in a closed matrix. Low shrubs (chamaephytes) also carry fire readily when they are dense, although they need a somewhat higher ignition temperature to burn. The latter condition certainly existed from the two fire causes (lightning and volcanic activity) that are present in Hawaii. Chamaephyte formations consisting of native shrubs can occur in Hawaii as seral stages of primary succession in the lowlands. Two important native shrubs in this category are Styphelia tameiameia and Dodonaea viscosa. The latter reproduces vigorously from seed after fire, while the former does not (Parman and Wampler 1977). Since Styphelia is the generally more dominant species, its fire behavior indicates that broadcast vegetation fires were probably not common.

Fire in Hawaii's Uplands

Here we may consider two important environments and vegetation types, the montane seasonal vegetation and the montane rain forest.

There is no doubt that natural fire played a role in the montane seasonal environments of Hawaii. These environments are present only on the two highest islands, Maui and Hawaii. The natural vegetation here contains several stand-forming native grasses including a native variety of the fire-resistant bracken fern, Pteridium aquilinum var. decompositum. The ecologically more important native grasses here are Deschampsia australis, Panicum tenuifolium, and Eragrostis grandis, mostly prevalent in the montane sections, and Agrostis sandwicensis and Trisetum cernuum in the subalpine to alpine sections. The latter rarely form closed grass matrices, whereas the three former species do. There are also several native sedges and light-adapted native ferns which contribute to the closed grass matrix.

In a study relating to the origin of the montane savanna and parkland formation on the east flank of Mauna Loa (in Hawaii Volcanoes National Park), charcoal was found in a soil pit at 70 cm depth (Mueller-Dombois and Lamoureux 1967). The charcoal was dated as $2,170 \pm 200$ years old. Thus, fire occurred in this environment before man ever arrived. This fire may have been started by a lava flow coming from the top of Mauna Loa and passing through already existing grassy vegetation there. The larger number of endemic grasses found in this area can be taken as evidence that grasses

were at a competitive advantage in this environment because they could recuperate quickly after mechanical damage. Undoubtedly, fire can be considered as one of the evolutionary stress factors in Hawaii.

It should be noted also that there are native tree species and shrubs in this montane seasonal environment, which form, together with the grasses, either parkland or savanna formations (Mueller-Dombois and Krajina 1968). The more important native tree species here are Acacia koa (koa), Sophora chrysophylla (mamani), and Myoporum sandwicense (naio). Koa, in particular, displays a high capacity to vegetatively resprout after fire. It has a root system not unlike that of aspen (Populus tremuloides) and resprouts readily from root suckers not only after fire, but also after release from herbivore pressure (Spatz and Mueller-Dombois 1973). It is also known that koa seed germination responds well to prior heat treatment (Judd 1920, Bryan 1929), which could be considered a fire adaptation. However, close relatives of this endemic phyllodial, nonthorny Acacia, occur also in Australia, and it is possible that the adaptive trait of heat stimulation of its seed was an adaptation of this genetic stock prior to becoming established in the Hawaiian environment. Mamani likewise responds well to fire by resprouting from the trunk. I don't know of particular observations on naio. But again the two shrub species, Dodonaea viscosa and Styphelia tameiameia occur naturally in the mountain parkland of Mauna Loa, and their responses to fire were already discussed.

Vogl (1969) emphasized that the Hawaiian montane rain forest shows fire adaptations in its dominant species, the 'ōhi'a tree (Metrosideros collina ssp. polymorpha), the tree fern (Cibotium glaucum), the mat-forming uluhe fern (Dicranopteris linearis), and others. In spite of close scrutiny, Vogl could not find any charcoal. He dismissed this point by saying that charcoal can be readily decomposed in tropical environments. Yet, in the cooler montane environment, decomposition is not rapid and charcoal would probably remain there for a very long time. Vogl pointed out that since the Pacific Northwest rain forest can burn, it should also be possible for the Hawaiian rain forest to burn. However, there is an annual dry season in the Pacific Northwest in July-August, and no such annual dry season is apparent in the Hawaiian rain forest environment. If anything, this speaks for a lower fire frequency in Hawaii. Year-to-year variations in rainfall do occur and Vogl pointed out that they can produce drought in the rain forest. He describes a situation in an east Maui rain forest above Hana in 1969 when mossy epiphytes, lichens, ferns, and the bark of 'ōhi'a trees had become so dry that upon igniting with a match, "fern, duff, green fern fronds, and surface forest litter produced a roaring fire" (Vogl 1969). However, burning over large areas has not (to my knowledge) been witnessed so far in the closed Hawaiian rain forests, only in seral or degraded stages, where large mats of uluhe-fern produce a combustible fuel (Anderson and others 1966).

A very new data base has just come forth that explains something on fire frequency in the montane Hawaiian rain forest on Mauna Loa. The data are here given for the first time with courtesy of the investigators, Lipman and others (1978).

A soil pit was dug near Olaa Forest Tract (Hawaii Volcanoes National Park) in an 'ōhi'a tree-fern rain forest growing on soil from volcanic ash. Charcoal was discovered in three sequential strata at 50 cm, 80 cm, and 130 cm depth. The samples were carbon-dated and gave as ages 340 ± 200 , $1,040 \pm 200$, and $2,080 \pm 200$ years. This shows that repeated fires have definitely occurred in certain sections of the Hawaiian rain forest. However, the fire frequency of 700- to 1,000-year intervals is low. It correlates with volcanism and not with drought years in these cases.

Volcanism is no doubt an important stress factor in the formation of Hawaiian vegetation. It includes fire as an associated stress, but volcanic ash fallout, which is a significant mechanic perturbation, can also and does more commonly occur without fires. It does not seem valid, therefore, to speak of adaptation to fire without

considering the primary perturbation complex. Ash fallout, which results in sloughing off leaves, branches, and bark of 'ōhi'a trees and in the defronding of tree ferns, has been observed in several situations near Kilauea Volcano (Doty and Mueller-Dombois 1966). Remarkable recoveries have been reported for these and other indigenous life forms and species (Smathers and Mueller-Dombois 1974).

As in Sri Lanka, where animal feeding has produced adaptive responses in the natural vegetation, in Hawaii volcanism has operated and still continues as an evolutionary stress factor. Both these factor complexes appear to also produce traits that can make such plants more resistant to fire. However, this form of fire resistance including that which results from adaptation to drought, i.e., xeromorphism, should be separated, wherever possible, from real adaptations to fire.

With occupation of the Hawaiian Islands by people and the advent and penetration of exotic grasses in many Hawaiian ecosystems, fire has recently become more important, but as a new disturbance rather than a natural stress factor.

TIME-RELATED CHANGES IN FIRE EFFECTS ON TROPICAL ECOSYSTEMS

Vegetation Potential and Fire

In a review paper on the ecology of grass fires, Daubenmire (1968a) emphasized that all studies of fire influences should be related to specific habitat types defined on the basis of their potential natural vegetation and described in terms of their current vegetation. Thus, if one had maps of current vegetation and potential natural vegetation and a certain knowledge of the fire regime of a region, one could perhaps predict something on the effects of fire in that region.

Potential natural vegetation is usually derived theoretically from the best developed natural vegetation remnant on a given habitat type. The habitat type itself is analyzed and described in terms of a number of factors (such as soil water, nutrient relations, etc.) which are normally hidden in the three basic site components, climate, soil, and topographic position.

It is difficult to generalize about fire influences on such a general level as attempted here. But the habitat and vegetation potential concept can be applied at any geographic scale. The term vegetation potential relates to the capacity of an area to produce a certain kind of vegetation (i.e., a combination of plants, species, and/or life forms, growing together). One generally thinks of three basic components that set certain limits to the vegetation potential of an area. These are the climate, the soil, and the floristic material available in an area (Walter 1971). Fire and herbivory are additional complexities which can and often do limit the vegetation potential.

Here I want to briefly examine to what degree fire may have entered into the constellation of these three basic components in the tropics during prehuman times.

In the preceding section I pointed out that there is general agreement among tropical ecologists that there is no grassland climate in the tropical lowland regions of the world. This implies that on all tropical soils, which have no special constraints in terms of their water and nutrient relations, one may expect a woody vegetation to develop, given enough time. This idea was reflected in the five major zonal tropical lowland ecosystems named in table 1.

However, it has definitely been established that certain tropical savannas are of natural origin. These lie in the middle of the tropical rainfall gradient. Sarmiento and Monasterio (1974) repeat a commonly asked question, which is, if tropical rain forests occur under wet conditions and thorn forests occur under the drier ones,

why do grass and herb dominated formations occur in the middle of this gradient? The answer is perhaps not so difficult. High rainfall favors woody life forms on nearly all soil conditions and grasses can be expected to be displaced rapidly by competition of woody life forms there, provided that fires are kept out and the site potential has not been reduced substantially. On the other side of the gradient one can say that since grasses root intensively in the upper soil surface, they cannot survive as well as the more extensively and deeper rooted thorn shrubs on well-drained arid soils. The problem of soil water relations among plant life forms in warm, arid zones has been dealt with in detail by Walter (1971).

The question of grass displacement in the absence of fire in humid areas is not so uncomplicated, however. Hueck and Seibert's (1972) map of the vegetation of South America shows campos cerrados patches, i.e., savanna vegetation, in the midst of the Amazon rain forest. There are also isolated Amazonian caatingas (low-stature open forests or woodlands with sparse grassy undergrowth). These correspond to the heath forests in the humid tropics of southeast Asia, and thus are more easily explained. This map, at the scale of 1:8 million, clearly is one displaying potential natural vegetation, i.e., habitat types or ecosystem types, not actual vegetation boundaries (Mueller-Dombois and Ellenberg 1974). However, in undisturbed areas, potential and actual vegetation boundaries may coincide. The presence of savannas in the Amazonian rain forest territory on this map indicates that these are considered to be stable vegetation types. Many of these Amazonian savannas are far away from any human habitation and they do not show any signs of human disturbance or fire. Similar isolated grassland and savanna patches are found in the Congo area of humid tropical Africa (Knapp 1973). Hueck (1966) argues that these Amazonian cerrados are relics of a formerly drier climatic period. Drastic changes of climate during the Quaternary from drier to more humid have also been emphasized for the African lowland rain forest territory (Vanzolini 1973). Webb (1964) has used the same argument to explain grass balds in the subtropical mountains of north Queensland. Southeast Asia apparently has not undergone any significant climatic change, and Whitmore (1975) believes this to be one reason for the greater tree species diversity in the tropical rain forest of southeast Asia.

One may wonder why these Amazonian savannas have such stable boundaries. Perhaps they are maintained by periodic lightning fires. But Sarmiento and Monasterio (1974) explain their constant boundaries on edaphic grounds saying that these relics are found on the nutritionally poorest latosols, which form a certain barrier for rain forest invasion even under the high rainfall regime.

This suggests that natural savannas may occur also in the humid tropics and that their presence there does not necessarily involve fires. However, the argument on whether fire does play a role in their maintenance has not been entirely settled (Sarmiento and Monasterio 1974).

Fire is also not necessary for the maintenance of the "hyperseasonal" savanna in the summer-dry and winter-wet tropical climate (zone II). There are very few tree life forms that can coexist with the grasses on such alternately flooded and totally dried up soils (Beard 1953). The most successful are palms, such as Copernicia and Borassus, which have intensive root systems not unlike those of grasses, but much magnified. Sarmiento and Monasterio (1974) point out that the extreme soil water regime is the limiting factor for a closed forest to become established and argue that if fire only was the limiting factor, such areas would become occupied by stands of pyrophytes.

However, the question may be asked whether the tropical environment and floristic material permitted evolution of true pyrophytes other than grasses. Blydenstein (1967) recorded fire-induced mortality even in Curatella americana, a thick-barked savanna tree of the Venezuelan and Colombian Llanos, which is considered highly resistant to fire. Moreover, savanna grass fires never generate such high temperatures

as do forest-humus fires (Daubenmire 1968a), under which many truly fire-adapted temperate trees survive. Woody plants resistant to fire can be found in many tropical dry forests and savannas. Budowski (1966) points out that these come mostly from more arid habitats. Their primary adaptation is therefore xeromorphism, which happens to also provide for fire resistance but which is not necessarily a true fire adaptation. Fire resistant trees can even be expected on the edaphically extreme soils in the humid tropics, such as on oligotrophic quartz sands, on ultrabasic, and on limestone soils. However, these edaphically more extreme ecosystems, which are characterized by some accumulation of raw humus on their soil surfaces, do not seem to "need" fires, for continued functioning as do some of the temperate forest ecosystems (Cooper 1961).

A different situation exists in the tropical montane environments of Central America and southeast Asia, where pine forests form seral stages (Knapp 1965, Whitmore 1975), and particularly in Australia where certain woody plant families, such as the Myrtaceae and Proteaceae, contain real pyrophytes (Beadle 1940). Both families have species with lignotubers, trunk buds, serotinous capsules, and heat-requiring seeds (Beadle 1940). However, again, the real forest fire and brush fire areas are in temperate and subtropical Australia (McArthur 1967, Hodgson 1967). In the tropical seasonal environment of north Australia one finds mostly open Eucalyptus forests with grassy undergrowth or savannas. Webb (1968) distinguished between the crown-fire region of the south and the grass-fire region of the north.

Thus, lowland areas in all tropical regions are characterized by grass fires, which under natural conditions had a low frequency (2 percent of all fires is a general figure given for natural fires for several regions, Walter 1960). Under these conditions true pyrophytes can be expected among tropical grasses, but certainly much less so, if at all, among tropical trees.

Consideration should also be given to the interaction of natural grazers and fire. The evolution of the Australian flora resulted mostly in evergreen sclerophyll species (dominated by the genus Eucalyptus) which often form canopies that allow much light to penetrate to the forest floor. This favored a combination of trees and grasses. However, a significant fauna of grazers did not result from the evolution of marsupials. The kangaroo, for example, is known as a rather extensive grazer with the outcome that no typically grazing-resistant grass life forms evolved in Australia (Walter 1960). Here, fire may have more vigorously assumed the role of the grazer in periodically reducing the grassy phytomass than in Africa, for example. On the latter continent, however, population fluctuations among the large herds of grazers may have provided inroads into forests, which changed some of these into woodlands or savanna woodlands. In this way, the natural grazers probably helped to spread fires into savanna bordering woodlands. Grazing can certainly reduce the frequency of fires; it can even eliminate fire altogether (Mueller-Dombois 1973a). Such reduction in fire frequency or local elimination of fire was possible in Africa, but not in Australia. The higher frequency and regularity of fire events in Australia may have aided in the evolution of fire-adapted woody plant life forms.

Successional Relationships

Succession can occur only where the fire frequency is low. This is rarely the case in the tropics today because once grasses have entered or have recovered in a tropical habitat, another man-set fire is usually soon to follow.

Here, I will first trace a few examples of fire-induced successions that have been reported to go back to forest, then I will try to extract a few principles.

FOREST FIRE SUCCESSIONS

Fosberg (1960) recorded some successional observations in savannas of the humid rain forest climate of the Micronesian Islands. These savannas are derived through

cutting the original rain forest and subsequent burning and cultivation followed by abandonment. The floristic composition of the savannas varies from island to island and from volcanic to limestone substrates. Their principal component, herbaceous matrix-forming life forms, are grasses (Miscanthus floridulus, Heteropogon contortus, Dimeria chloridiformis), sedges (Fimbristylis, Scleria, Rhynchospora,) and ferns or relatives (Dicranopteris linearis, Lycopodium cernuum). Shrubs, such as Melastoma malabathricum, Pandanus, and Morinda pedunculata, are of scattered distribution. Their presence or absence is usually a function of fire frequency. Miscanthus, the sword-grass, is often the dominant grass under frequent burning. In the savannas of Guam, which were not allowed to be burned during the Japanese occupation in World War II, young forests of ironwood (Casuarina equisetifolia) had appeared. However, a few years later between 1950 and 1957, these forests disappeared again, because fire had been set frequently in spite of laws against it.

In this case rapid forest recovery was observed, but only by an introduced species, an obvious pioneer, that assumed the same role on Krakatau (Richards 1952) and in Hawaii on lowland volcanic ash (at Kapoho). Casuarina clearly is a fire-susceptible species on account of its poorly decomposing, raw humus-forming leaf litter. But it has not much resistance to fire. Thus, renewed fire activity resulted in a rapid retrogression.

Kowal (1966) made observations of succession in a montane seasonal environment in Northern Luzon, Philippines. Here he found three major vegetation types at lower and middle elevations (1 000 to 2 400 m), a broad-leaved montane forest, a pine forest (dominated by Pinus insularis, with P. merkusii as subdominant associate), and grassland. The pine forest and grassland had originated from fields abandoned after 2 to 3 years of shifting cultivation. Kowal says that this secondary pine forest is subject to frequent surface burning, because of its grass-dominated undergrowth. These fires occur normally at intervals of 1 to 5 years and result in thin litter and highly eroded soil. The pine trees survive under these conditions. A distinct trend from xeric to mesic undergrowth vegetation was observed in different stands of the pine forest on similar soils where fire had been kept out. Under these conditions, the undergrowth vegetation (with Miscanthus sinensis and Eupatorium adenophorum as dominants) had become taller and denser. New pine seedlings were suppressed and montane broad-leaved forest species began to enter. Kowall concluded that wherever fire is eliminated after abandonment there is a succession from Miscanthus grassland to pine forest to montane forest of similar composition as in primary forests.

A similar, but somewhat more complicated, succession involving pine savannas was reported by Munro (1966) in Central America (Nicaragua). Here, Pinus caribaea forms lowland savannas in the tropical transition climate (zone I-II). Munro suggests a cyclical pattern of development in seven phases from the original, relatively uninflammable tropical hardwood forest, through a man-altered "fire-penetration phase" in which Pinus caribaea is present, to a rapidly formed pine savanna with only grasses as the second life form. The latter is maintained through frequent burning (annual or 4-year interval burning). Different recovery phases are recognized on the basis of burning frequency, such as burning at 5-year, 25-year, 80-year, and 140-year intervals. In the latter three phases the original hardwood species return as undergrowth and finally form the dominant tree components. Munro's scheme is only a hypothesis developed from observations of side-by-side differences in vegetation with different burning regimes. However, most successional conclusions are derived in this way and, if done carefully, they can give a realistic picture.

Whitmore (1975) provides a generalized successional scheme for the lowland dipterocarp rain forest in Malaya, which is as follows: Upon clearing, primary dipterocarp forest becomes replaced by a Paspalum conjugatum grass association. If there is no burning, this will be invaded by young secondary forest. The woody species are pioneers, which establish from seed after the gap is formed, not from preexisting

seedlings. The secondary pioneer vegetation includes giant herbs, such as gingers and bananas, tangles of woody heliophytic climbers (Merremia, Uncaria). These become invaded by light-demanding, fast growing trees, often belonging to different species of the pioneer genus Macaranga (Euphorbiaceae). Most of these are big-leaved (megaphyll) trees, which belong to such families as Euphorbiaceae, Malvacaceae, Moraceae, Sterculiaceae, Tiliaceae, Ulmaceae, or Urticaceae. These pioneers are later replaced by shade-tolerant, more slow-growing seral and climax dipterocarp species.

However, if the first pioneer grass, Paspalum conjugatum, is burned, a real pyrophyte becomes quickly established. This is the grass Imperata cylindrica, which has rhizomes from which it can almost perpetually reestablish after annual or more frequent fires. Once Imperata cylindrica is established, succession does not proceed to forest unless special precautions are taken to prevent recurring fires.

Another successional route is taken upon the first pioneer grass Paspalum, when this grass is subjected to grazing instead of firing. Upon grazing, creeping grasses become established, such as Chrysopogon aciculatus, Axonopus compressus, and the low mat-forming herb Desmodium triflorum. Such a grassland association of low-growing and continually cropped pasture life forms becomes more or less self-protected against fires.

Thus, three important grassland associations can develop from clearing primary dipterocarp forest. One of these is a grass pyrophyte association, which results from the first burning. Whitmore states that forest cutting followed by burning and the cultivation of only one crop permits reestablishment of the forest. But repeated cultivation and burning results in site deterioration, soil erosion, and the development of shrub stands of Melastoma malabathricum, Lantana camara, and others. Frequent burning leads ultimately to a grassland of Imperata cylindrica. In tropical America a parallel role is assumed by Imperata brasiliensis (Beard 1946). Whitmore (1975) points out that bamboo thickets commonly form in fire climaxes in southeast Asia. But they must be related to a lesser fire frequency. Apparently, there is as yet a great gap of knowledge in the area of secondary succession and secondary forest formation in tropical rain forest areas.

Brinkman and Viera (1971) report on seed survival after experimental burning of a young secondary rain forest in the Amazon area near Manaus. Seeds of 31 Amazonian rain forest species were planted at various depths, ranging from 2 to 20 cm into mineral soil under a 10- to 12-year-old secondary forest. A simulated slash burn resulted in 100 percent seed mortality at 2-cm depth and 90 percent mortality at 5-cm depth, indicating the low heat tolerance of primary forest tree seeds. The authors conclude that forest succession after slash burning will be almost exclusively from airborne seed, a conclusion which supports Whitmore's (1975) observations in southeast Asia.

In derived (i.e. anthropogenic) savannas in the subhumid transition zone (I-II) of tropical Africa a few observations and experiments illustrate succession back to forest under exclusion of fire.

Schmidt (1973) studied the plant communities of the Lamto Nature Reserve (about 100 km north of the Ivory Coast). Within a section of the Hyparrhenia savanna, which had been protected from fire since 1962, he found a significant invasion of woody plant species of the deciduous forest, of which remnant stands occurred nearby. He defined five variations in the Hyparrhenia savanna, which were distinguished by increasing densities of woody plants. He concluded that under protection against fire, there is a fairly rapid succession leading back to a near-original forest climax stage. A similar conclusion was reached by MacGregor (1937) through a study of experimental burning and fire exclusion in Nigeria.

In the same climatic transition zone (I-II), Lock (1977) did an experimental exclosure study in Kabalega (formerly Murchison Falls) National Park, Uganda. Here, the combined effects of elephants and fire result in the replacement of Terminalia glaucescens woodland by Hyparrhenia rufa grassland with scattered Lonchocarpus shrubs. Also the Cynometra high forest is similarly reduced. Lock studied two 60 x 60 m plots which were established in grassland derived from Terminalia woodland. Both were surrounded by a firebreak and one of them also by an elephant-proof ditch. Vegetation was periodically recorded over a decade. Woody plant regeneration was found to be much greater in the double protected exclosure. Lock found the species composition to recover more in the direction of the woody species normally found in the savanna (Albizza, Combretum, Terminalia) than in the direction of the local Terminalia woodland, and he doubts that the original woodland vegetation will be restored.

A very slow and imperceptible succession was observed by Blydenstein (1967) in the Llanos savanna in Venezuela and Colombia which lies in the strongly seasonal tropical climatic zone II. He encountered tree grove development in some areas, which seemed to start from the establishment of fire-tolerant tree species such as Byrsonima crassifolia, Curatella americana, and others. These may form a nucleus for grove development when protected from frequent fires. Other less fire tolerant woody species can become established in their shelter and soon an outer ring of xeromorphic shrubs is formed. The grove trees are then better protected from fire and the grove interior provides for a more mesic ecoclimate under which other more mesophytic woody plants can become established. However, Blydenstein points out that the groves hardly expanded in size. He made measurements on successively taken airphotos and found that there was hardly any increase in grove size over an 11-year period. The species composition of the groves was different from that of nearby forests indicating a deflected succession. Moreover, the less heat-tolerant grove species were in some cases destroyed by a single fire when the parkland area was no longer protected from fire.

SOME PRINCIPLES

These examples show that forest fire successions in the tropics rarely start from natural causes. They usually originate from logging or shifting cultivation and subsequent man-caused fires. Naturally induced fire successions may have occurred in Africa, where elephants can open up a forest by pushing trees to the ground. However, such events of forest destruction may be the outcome of concentration effects or local overpopulations due to only recently established management practices (Buechner and Dawkins 1961).

Secondary successions after fire are usually rapid (one to a few decades) in the humid rain forest zone, once fire is eliminated, but they are rather slow in the tropical seasonal climate. Here in turn they may be quickly eliminated because of the overwhelming presence of grass areas around them. The length of the dry season is a very important factor in forest recovery. Regardless of the tropical climatic zone (i.e., humid, transitional, or strongly seasonal), the first effect of fire after forest cutting is the invasion of graminoid life forms. In the humid tropical lowlands this is usually the rhizomatous tallgrass Imperata. Thus, fire after logging increases the fire hazards in tropical forest habitats. This is an important contrast to the temperate forest habitats, for example in the Pacific Northwest, where slash burning is practiced for the purpose of decreasing the fire hazard.

Although there are indications that the original species composition may become reestablished once fire has been eliminated, there are, as yet, no data to prove that this is so. Secondary forests reestablished after fire are usually quite distinct. However, this may not be so much a function of the fire itself as of the original perturbation in the form of shifting cultivation, which usually results in a lowering of the nutrient potential. Most studies of fire successions indicate "deflected"

successions in the sense that they result in a different tree species composition. This is not necessarily the result of a lowered site potential, but perhaps a function of the changed spatial relationships after denudation. Certain seed sources may be so far away that the original composition cannot be reestablished. Moreover, certain trees may have entirely disappeared from an area, resulting in a lowering of the floristic potential.

There are several tropical grassland successions reported in the literature (Whyte 1968, Gillison 1969, Kartawinata and Mueller-Dombois 1972, Balakrishnan 1977), but there is no room to discuss them here. They may, moreover, be looked at merely as dynamic fluctuations in response to changing fire frequencies (Vogl 1969).

Ecosystem Conversion and Degradation

Successions back to forest after the use of fire are exceptions in the tropics. The much more common phenomenon is conversion from forest to savanna or grassland. Because of the very low inflammability of tropical rain forest (see also Mutch 1970), the forest conversion to savanna or grassland is rarely direct. Where direct fire conversion is involved, it is usually a very slow or gradual process that begins with scorching and killing nonresistant trees at the forest border to the savanna (Aubreville 1949 cited in Bartlett 1955, Mueller-Dombois and Perera 1971). Of course, one can consider this direct form of forest border reduction also as fast, depending on the time scale one wishes to use.

Nevertheless, the most rapid conversion comes through forest cutting and shifting agriculture, and as commonly reported from Africa (Buechner and Dawkins 1961, Laws 1970, Ross and others 1976) through elephant activity, when elephant density outgrows the local carrying capacity of the ecosystem (Mueller-Dombois 1973a).

Richards (1976) writes, "There is abundant evidence that in most of West Africa, as well as in other parts of the continent, the closed forest has retreated and the savanna advanced during recent times." The conversion is continuing and in some parts, the savanna is displacing forest at a rate of 1 km per year. Phillips (1974) gives Aubreville's estimates adjusted for 1974 separately for each major area in tropical Africa, and says that only 60 percent of the potential area is left under forest; further, that over half of what is left is altered by shifting cultivation and other forms of exploitation. This means that less than 30 percent is left in primary forest in tropical Africa.

Whitmore (1975) gives a similar picture for the tropical forest of southeast Asia by saying that all formations have been in part degraded by man. However, in southeast Asia this refers only to the use of forest territory for shifting agriculture, not to the savanna conversion, which certainly has been much more severe in Africa. This is confirmed by a comparison of the vegetation maps of van Steenis (1958) for Malaysia with that of Keay (1959) for tropical and south Africa, which both show the areas of derived savannas.

The important question relating to ecosystem conversion in the tropics is to what degree this process is reversible. Information on this aspect is as yet very incomplete and controversial (Qureshi 1978). Clearly, tropical forests can reconstitute themselves when disturbed from natural causes, which only in a few exceptional cases (e.g., heath forests, tropical pine and oak forests, teakwood forests, eucalyptus and paperbark tree [*Melaleuca*] stands) involve fire as a rejuvenation mechanism.

Two aspects appear significant in the question of reversibility of tropical forest ecosystems when converted with the use of fire. One aspect relates to the length of time the ecosystem has been converted, the other to the size of the area and its spatial relationship.

Whitmore (1975) states that "felling, followed by burning and the cultivation of a single crop, allows reestablishment of forest." Most areas under shifting cultivation in the humid tropics are abandoned after 2 to 3 years (Bartlett 1955, Hueck 1966). Secondary forest can still reinvade such areas (Fosberg 1960, Kowal 1966), but it is not known whether trees can gain the original size on those habitats. There are many examples where shifting cultivation has led to reinvasion of woody vegetation with lesser height potential (scrub vegetation, Knapp 1965, Walter 1971), which appear to form a stable end stage, a disclimax. Brinkmann and de Nascimento (1973) report on the effects of tree felling with subsequent burning in the Amazon forest on latosols near Manaus and say that although large amounts of nutrients are rapidly released to the soil after burning, much is lost by leaching or becomes fixed and therefore is lost from the site potential. If felled trees are burned in situ as is the common practice in shifting agriculture, there is clearly a temporary nutrient enrichment, although accompanied by simultaneous losses, particularly from leaching. But where the tree crop is extracted, the nutrients are largely removed together with the trees (Walter 1971), and the site potential is significantly reduced resulting in more or less permanent site degradation. This, of course, is not the result of burning, but a consequence of removing the phytomass.

Krebs (1975), however, working in a humid tropical area of Costa Rica found a less drastic site deterioration after forest conversion to agriculture. In this area forest was replaced by pasture, sugarcane, and coffee. In sampling soils under forest, pasture, and crop fields, she found organic carbon values to be significantly (but not drastically) lower under pasture and crop fields. This was expected since, for example, organic matter returns from sugarcane were $0.8 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ versus 1.1 kg in the forest. Total nitrogen and organic carbon values decreased significantly from forest to crop fields, but then remained stable over time. Available Ca decreased from 600 ppm to 200 ppm in fields over a period of 22 years, while Al increased from 800 to 1 200 ppm. She concluded that while there is definitely a slow soil deterioration, it is not as serious as often assumed. Apparently, permanent agriculture is possible in this area. However, the soil there is of volcanic origin with alluvial material overlying lateritic deposits. Moreover, the study area has an elevation of 500 m to 1 000 m with a mean annual temperature of 23° . It is thus not a typical humid tropical lowland area with aged latosols. Blydenstein (1968) warns of sweeping generalizations about site deterioration upon cropping and burning in the tropics.

This is indeed an important point. What clearly is needed are ecological classifications and maps of habitats and potential natural and existing vegetations in all the major tropical regions. This was already strongly emphasized by Daubenmire (1968a).

Site degradation upon conversion of forest to savanna is apparently also not so serious in the seasonal tropics as it is in the typical humid lowland tropics. Daubenmire (1972) made a thorough ecological habitat analysis of a semideciduous forest and a 22-year-old Hyparrhenia rufa savanna occurring adjacent to each other in the seasonal lowland of Costa Rica. The soils under the two vegetations were of the same basic materials, but the savanna soil had become much more stony at the surface. The upper 10 cm of soil yielded 83 percent peds on a 2 mm screen from the savanna as compared to 38 percent from the forest. The infiltration rate under forest as compared to the savanna was 47:1, indicating that a much less permeable soil had formed under conversion to savanna. During the dry season, the savanna soil showed many more and wider cracks than the forest soil. The forest soil contained earthworms which were absent in the savanna soil. The infiltration rate under forest as compared to the savanna was 47:1, indicating that a much less permeable soil had formed under conversion to savanna. During the dry season, the savanna soil showed many more and wider cracks than the forest soil. The forest soil contained earthworms which were absent in the savanna soil. A great difference was found in the permanent wilting percentage at 50 cm depth, where the savanna soil showed 23.5 percent, and the forest soil 15 percent. Total nitrogen was lower throughout the profile in the savanna soil, the difference in the surface soil being 0.1 percent in the savanna and 0.4 percent in the forest. The organic carbon values in the upper 10 cm were 2.8 percent for the

savanna and 3.5 percent for the forest. Although the overall nutrient content was somewhat lower in the savanna soil, the chemical differences were less important than the physical differences, which had deteriorated significantly under the annually burned savanna. The most important factor appeared to be surface soil erosion, which was estimated from pedestalled Hyparrhenia plants and other indices to have been 11 cm during the 22-year period on a 9 percent slope in the savanna. Soil erosion is also the most important site deterioration in broomsedge (Andropogon virginicus) savannas on humid windward Oahu (Mueller-Dombois 1973b).

Daubenmire concludes from his analysis that soil deterioration under savanna had not yet progressed to a stage where forest reestablishment was difficult. With a prolonged stage of conversion under savanna, erosion further deteriorates the site potential, and iron hardpan formation (Budowski 1956) and very poor permeability (Joachim and Kandiah 1942) may signify the ultimate stage of site degradation.

However, there are situations where forest reinvasion (as differentiated from artificial reestablishment) into grassland does not take place even under fire protection. In the montane grassland of Sri Lanka, the black patana, forest re-invasion has never been observed even where the savanna was protected from fire for a long time (Mueller-Dombois and Perera 1971). This is in a rain forest environment where forest succession could be expected to follow the grass stage. De Rosayro (1946) suggested that frost may be involved in preventing invasion of seedlings from the adjacent montane forest.

In a study of succession on abandoned fields in the black patana (Balakrishnan 1977), no tree seedlings were observed to invade abandoned fields even next to the forest border over at least a decade of protection from fire. The succession on abandoned fields progressed from annual weeds and grasses to mat-forming perennial herbs (Cyanotis pilosa, Centella asiatica) to a bunchgrass (Chrysopogon zeylanicus, Arundinella villosa) stage with scattered woody chamaephytes (Gaultheria rudis). At this point in time the succession appears arrested. A tree with lignotubers and cablelike roots, Rhododendron zeylanicum, occurred scattered in areas which were protected from fire for longer periods. This tree is fire adapted and has a mechanism via its cable roots to establish itself vegetatively from below the grass sod. A similar mechanism occurs in the Hawaiian Acacia koa (Spatz and Mueller-Dombois 1973).

Natural reinvasion into a grassland or savanna requires special adaptations in trees. Such adaptations may not have evolved in the forest trees adjacent to a derived savanna.

SPATIAL RELATIONSHIPS

Relatively small openings, called "gaps," in tropical rain forests, signify local breakdown stages accompanied by rejuvenation, i.e., small area successions or "serules" (Daubenmire 1968, Poore 1968). Such openings, which can be up to 1 ha in size (Brünig 1964), are a natural phenomenon in the maintenance behavior of certain tropical forest ecosystems. Predictions of successional events following a perturbation are vague without a consideration of the spatial relationships (Mueller-Dombois and Ellenberg 1974).

Therefore, the spatial dimensions of a forest conversion should not be ignored. The effects of soil erosion are very much magnified in large-area logging operations (Webb 1977). On tropical latosols the property of irreversible drying of the poor oxide clays, which turn at the surface into bricklike secondary rock particles, is much aggravated by enlarging the size of the converted area. Hardpan and ironstone formation has been of particular concern in derived savannas (Budowski 1956).

Another spatially related degradation resulting from conversion relates to a loss in floristic potential. This type of loss may occur at two levels. In the coastal lowland of Hawaii Volcanoes National Park, "exhaustion of seed supply" from suitable indigenous woody plants has occurred. The area represents a well-defined tropical seasonal grass and shrub savanna ecosystem which in this case was not necessarily derived from fire, but from the release of domesticated goats, which became feral and were active in this ecosystem for the past 150 years (Mueller-Dombois and Spatz 1975). Degradation of this ecosystem proceeded in some parts to barren soil and an annual grass stage, characterized by the dominance of the pantropical lovegrass, Eragrostis tenella. Experimental exclosures resulted in a quick recovery of first, perennial mat-forming grasses (Cynodon dactylon, Digitaria pruriens, Melinis minutiflora), then bunchgrass (Rhynchelytrum repens, Heteropogon contortus, Hyparrhenia rufa), woody chamaephytes (Indigofera suffruticosa, Cassia leschenaultiana, Waltheria americana), and in certain areas, indigenous vines (Canavalia kauensis, Ipomoea congesta). The area, with an annual rainfall between 800 and 1 200 mm, has a potential for tree growth, where not covered by too recent lava flows. Weed-tree species (Leucaena latisiliqua, Ricinus communis), which are as yet confined to local areas, have a potential to invade the area. They are controlled by the Park Service from spreading as much as possible.

The succession following goat exclusion proceeded to the bunchgrass-chamaephyte stage within less than 5 years. It is now arrested in this stage, because suitable indigenous trees are no longer in the area for reinvasion. Although there are native 'ohi'a (Metrosideros collina ssp. polymorpha) and ebony (Diospyros ferrea) trees left scattered in some parts of the area, their ecological properties are such that they cannot invade as seral trees into an advanced bunchgrass-chamaephyte stage.

Therefore, not only can indigenous trees be eliminated by prolonged herbivory of their seedlings and saplings, the elimination may involve certain ecological types of trees, without which a recovery to forest cannot proceed.

In this process, herbivory and fire can be compared as mechanical factors of reducing potential genetic stock for recovery. Although I did not find any specific records, there is little doubt that large-area conversion of forest to savanna with the use of fire, as has happened and is continuing particularly in Africa, has reduced the genetic potential and diversity of tropical forest trees suitable for recovery under natural conditions. Thus fire in the lowland tropics in particular can be seen as a threat to the rarer tree species resulting in irreversible losses of floristic potential.

However, forest conversion to savanna has been an economically profitable practice in some tropical areas even on a long-term sustained-yield basis (Lemon 1968). In such areas, particularly in the montane tropics, controlled burning may be practiced to improve foraging values without any further effects of degradation. This applies also to the forest value of certain pine savannas (Munro 1966), or to combined values of foraging and tree production (Gregor 1973). In some instances the productive capacity of derived savannas is enhanced or at least maintained by the use of fire (Lamotte 1975, San Jose and Medina 1975).

Thus fire in the tropics is certainly not all bad as has been clearly pointed out also by Phillips (1965). In the pyrophyte vegetation of the tropics, i.e., in savannas and certain tropical pastures, but also in certain pine, paperbark, eucalyptus, and teakwood (Tectonia grandis, Puri 1960) stands, fire can be a useful management tool. However, this is a different topic, which was not intended to be covered in this paper.

SUMMARY AND CONCLUSIONS

The foregoing review has given some answers to the three basic questions posed in the Introduction. These answers will be summarized under three subheadings.

Fire Relations Along Spatial Gradients of Tropical Ecosystems

Spatial ecosystem gradients and fire were examined in a latitudinal perspective for the tropical lowlands, and altitudinal gradient examples were discussed for Sri Lanka and Hawaii. The latitudinal trends were summarized in table 1.

The zonal vegetation on normally drained soils in the tropics is regarded by most ecologists as potentially a woody vegetation. This vegetation was here defined at a general level into five major zonal ecosystems in relation to a climatic moisture gradient from wet to dry as rain forest, semideciduous forest, dry-deciduous forest, and desert scrub with succulents. A fifth major zonal type is the monsoon forest of southeast Asia and north Australia, which includes evergreen sclerophyll and mixed evergreen-deciduous forests in the same range of climatic seasonality as defined for the semideciduous and dry-deciduous forests in tropical America and Africa.

There are also several important intrazonal ecosystems in the tropics, in which the dominant control factor is either an extreme soil variation or man. Important soil variations in the rain forest terrain are podzolized sands with heath forests, forests on limestone or serpentine, peat-swamp forests, and others. Except for the peat-swamp forest, fire has been recognized as a natural factor in these edaphically extreme rain forest ecosystems. The basic reason for this appears to be an impeded soil microorganismic activity, which allows the accumulation of some raw humus in those forest types. The raw humus provides enough fuel to carry surface fires. However, because of the continually wet climate and the relatively small amount of raw humus accumulation, which may be quite discontinuous on the floor of such forests, both fire frequency and intensity were probably very low under natural conditions. Where fire has been used in such forests, they are easily degraded to shrubland or savannas with sparse open grass covers.

A very important natural fire type in the tropics appears to have been the alternately inundated and extremely dried up "hyperseasonal" savanna. It still is an important fire vegetation today, although others have become even more important through the influence of man. These are the derived or anthropogenic savannas found today widely distributed throughout the territory of the rain forest, and semideciduous, deciduous, and monsoon forests, but almost absent in the tropical desert areas. On an area basis they are today more important than the forest vegetation, at least in Africa and America. North Australia may form a special case, where significant areas of fire-originated savannas probably predate the use of fire by man. This is perhaps related to the more open canopy structure of Australian sclerophyll forests which allows a grassy understory to develop. Fire-adapted woody plant life forms are particularly common in this part of the tropics.

In an altitudinal perspective, fire in the tropics also follows wherever the most combustible plant life forms, namely grasses, form vegetation types. In addition, montane forests, like temperate forests, accumulate a certain amount of humus on the forest floor. For this reason, tropical montane forests are more prone to surface fires than tropical lowland forests in general. However, montane rain forests cannot be considered a fire-adapted vegetation, because of the absence of rainfall seasonality. Fire-resistant plant life forms with vegetative resprouting capacity may have evolved in Hawaii in this wet environment primarily in relation to the effects of volcanism, and in Sri Lanka primarily in relation to the large herbivores in its ecosystems. These mechanical stresses may have worked in a similar direction as periodic stresses due to fire. Therefore, fire resistance should not be equated with fire adaptation.

Fire in Relation to Vegetation Potential, Tropical Forest Succession, and Retrogression

Vegetation potential, which is generally considered a time-dependent function of climate, soil, topography, and floristic material available in an area, can be modified considerably by fire, but also by grazing. The question of the degree with which fire and grazing, or its combinations, have modified the three basic habitat components (climate, soil, and topography) is best answered through a knowledge of potential natural vegetation in relation to the existing vegetation and an analysis of the site potential. The spatial and temporal variations and impacts of fire in ecosystems cannot be properly evaluated until information on site potential, existing and potential vegetation is established. This point was emphasized by Daubenmire (1968a), because of the variable effects of fire which make any prediction difficult. This plea is repeated here particularly for a rational approach to land management in the tropics, where such ecologically based land and vegetation inventories are rarely available.

Therefore, little predictive information can as yet be given on the question of whether or not and to what degree forest conversion to savanna or grassland is reversible. A few observations on forest succession following fire are available in tropical rain and seasonal forest areas. When the area is not too large and not converted for too long, natural forest reestablishment appears possible in tropical forest areas. However, in larger sized forest conversions, there is a rapid site degradation in tropical rain forest areas in terms of erosion, loss of nutrient potential, and deterioration of soil-physical properties (particularly ironstone formation). Site deterioration processes are also indicated for seasonal forests, but on a less rapid time scale.

Another significant degradation, especially in relation to the size of the forest conversion, appears to be the loss of floristic potential. Large-scale forest conversion may result in the removal of species with a capacity to invade a grassland. Loss of tropical tree species diversity and therefore loss of genetic potential in general is an almost predictable outcome in all tropical countries where fire is not brought under control.

In contrast, controlled use of fire in tropical grasslands and pastures may be employed in some derived and natural savannas and grasslands. However, there seems to be little useful application of fire in tropical forests except in special types, such as pine woodlands, teakwood plantations, and in some tropical Australian forests with fire-adapted woody plants.

Differences Between Tropical and Temperate Ecosystems

The fundamental functions of fire are the same in all regional ecosystems of the world. Fire can act as a destroyer of plant life and associated biota. It can also function as ecosystem rejuvenator. Fire causes damage from heat but also stimulation of root suckering in some trees or resprouting in rhizomatous and bunchgrasses. It induces the opening of serotinous fruits and seed germination in fire-adapted species. Fire, moreover, acts as substitute consumer, where large herbivores are eliminated from an area or where they do an insufficient job, and fire supplements the function of decomposers where they are inhibited in some cases due to waterlogging or extreme drainage, strong temperature seasonality, poor nutrient status, or toxicity of the soil.

Fire frequency and intensity are fundamental variables in the negative or beneficial effects of fire. However, every region has its own peculiarities and the role of fire varies between regions, but also within each region from habitat to habitat. A great deal has been learned from fire research and management in temperate

and subtropical ecosystems, but fire management practices found to be successful in those major world regions should not be extrapolated and applied automatically also to the tropics. There is a greater resemblance in the montane tropics with temperate and subtropical fire relations, but even here extrapolation can lead to mismanagement.

The lowland tropical forests are fundamentally different from temperate forests in their fire relationships, since tropical lowland forests do not accumulate organic matter at their forest floors, except in a few cases where tropical lowland forests grow on extreme soil substrates. Therefore, it cannot be said that an occasional fire is needed in those ecosystems to produce a rejuvenating perturbation.

This is not to say that tropical forests are not exposed to periodic perturbations. On the contrary, maintenance mechanisms in tropical forests often involve violent perturbations, such as hurricanes (Whitmore 1969), tree-group-killing lightning discharges (Anderson 1964), often combined with wind breakage (Brünig 1964), flooding (Hueck 1966), or more subtle perturbations, such as possibly rare soil-surface droughts in rain forests (Mueller-Dombois and others 1977). Very little is known as yet about the maintenance behavior of tropical forests under natural conditions but this knowledge is vital for proper forest management. This has been clearly demonstrated through the complexities of fire relations in temperate forests.

Fire in tropical ecosystems is mostly related to the distributional trends of the grass life form. Where this plant life form has been encouraged to penetrate into forests, fires have followed. In Australia this has probably occurred over a very long evolutionary time scale before man became a dominant factor. Therefore, there are probably more fire-adapted tree and shrub life forms found in the Australian tropics than elsewhere. There are also many fire-resistant tree and shrub life forms found in other tropical regions, but their fire resistance may be the outcome of adaptations to periodic drought (xeromorphy), herbivory (vegetative resprouting capacity) storm damage, volcanism, or other perturbations.

A major difference, though not discussed in any detail in this paper, is the greater soil-nutrient stability of temperate versus the soil-nutrient fragility of tropical forest soils. The latter is extreme in lowland tropical rain forest soils. Fire, though usually not the initiating factor, causes, in combination with felling and shifting cultivation, rapid site degradation. However, the physical site degradation in terms of erosion and ironstone formation can be an even more important damage. The destructive effects of fire are further aggravated, if fire is used for slash burning after extractive logging operations in the humid tropics. Fire in tropical forests invites more fires, because of the almost immediate invasion of pyrophytic grasses (such as Imperata).

A different situation exists in tropical savannas and grasslands. Here, fire, if used wisely, may even enhance productivity and the foraging value. However, derived savannas are in most cases already degraded sites and fire can easily promote further degradation if not controlled carefully.

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SECTION I

INTEGRATING SUMMARY

The papers in this section document the complex relationships between fire regimes and fire effects in a variety of ecosystems. Using Heinselman's classification scheme, fire intensity ranges from surface fires that move slowly through vegetation to fast-moving crown fires. Fire frequency, measured as the return interval between fires, may be as short as 1 year or may extend into centuries. In every presentation the point was made that fire intensity and frequency are not independent variables. Areas with short return interval fires tend to have less intense fires than areas with long return interval fires. Moreover, many ecosystems are subjected to low-intensity, short return interval fires as well as less frequent, high intensity fires. The relationship between frequency and intensity is complicated by a variety of factors such as vegetation structure, productivity, weather, and topography. Grasslands, for example, can support high intensity fires that burn annually.

Both Heinselman and Kilgore emphasized that fire frequency and intensity must be defined precisely if comparisons between studies are to lead to any meaningful synthesis. Kilgore proposed that "fire frequency" be used only in reference to the fire return interval at a particular location, whereas "fire incidence" should be used to refer to the interval between fires which burn within a specified land unit but not necessarily at the same point. Clearly, statistics such as the number of fires per million hectares per year say very little about the probability that a wildfire will occur at a particular location within a forest. It may be more difficult, and perhaps undesirable, to arrive at a conventional definition for fire intensity. If the focus of an investigation is on energetics or fire behavior, as in several current attempts to model fire spread, then fire intensity is best defined in terms of energy released per unit time per unit of fire front. An investigator interested in carbon or nutrient cycling, or fuel reduction, may prefer to express fire intensity more simply as energy or biomass consumed per unit area. These measures may or may not be of use to researchers concerned with the impact of fire on ecosystem biota. For example, low intensity surface fires in ecosystems composed of vulnerable species, such as white cedar swamps and mesic cove forests, result in substantial changes. In contrast, high intensity crown fires in chaparral or lodgepole pine forests can simply stimulate reproduction of the same species which were burned with little compositional change.

An interesting circularity is obvious in the processes described in all of the papers. Not only do different fire regimes result in variations in ecosystem structure and development, but these same ecosystem characteristics significantly influence fire frequency and intensity.

A variety of abiotic components of ecosystems regulate fire frequency and intensity. Climatological variables influence fire variations on a geographic scale. The frequency of lightning discharges and associated rainfall are the most important variables influencing ignitions in some ecosystems. However, in other ecosystems man has and still does control the frequency of fire starts. In general, fire frequency increases inversely with moisture availability. On the other hand, in very dry areas, such as the short grass prairie and the sandhills low productivity and consequent slow rates of biomass accumulation can result in longer fire return intervals. There are other abiotic ecosystem components that also influence fire frequency and intensity. For example, clay soils tend to retain water near the surface, thus keeping fuel moisture content relatively high and, as a result, the frequency of ignitions is kept low.

The role of topographic diversity and vegetation pattern in regulating fire frequencies in any given area has been emphasized in each paper. When vegetation

provides a continuous covering of fuel over a relatively unbroken landscape, fires tend to be much larger and, therefore, fewer successful ignitions are required to produce a given fire frequency. The roles of natural barriers, such as wetlands, streams, and lakes, have also been emphasized. In addition, developments in areas such as the prairies, the Atlantic Coastal Plain, and tropical grasslands, break up vegetation with roads and agriculture and alter the normal spread of fire.

Vegetation characteristics also influence both fire frequency and intensity. In many temperate ecosystems fuels tend to accumulate as vegetation ages. Furthermore, the quality and distribution of these fuels also change. In many grassland, shrubland, and forest communities the ratio of dead to live biomass increases with time. This change is a consequence of slow rates of decomposition which may result from xeric conditions, as in chaparral, or perennially wet conditions, as in evergreen shrub bogs. Such an accumulation is often associated with the production of sclerophyllous leaves and ligneous litter. In any case, such changes act as positive feedback mechanisms that increase the likelihood of successful ignitions. However, many ecosystems, such as mesic deciduous forests and tropical forests approach a relatively low steady state fuel mass and no such feedback is apparent.

Inherent qualities of fuel, such as density and secondary chemical content, may alter its flammability. Such alteration could obviously affect the probability of ignition as well as the intensity of fires when they occur. It seems at least possible, as Mutch (1970) has suggested, that natural selection could act on these characters to maintain optimal fire frequencies.

Changes in vertical and horizontal fuel distribution associated with ecosystem development affect both fire intensity and frequency. Given sufficient time between fires, understory trees and debris form a vertical pathway, or "ladder," of fuels from the forest floor to the canopy along which fire may be carried into the crowns. A corollary to this general trend is that frequent fires tend to produce widely separated vertical strata in forest ecosystems, as has been shown in the western ponderosa pine forests, northern coniferous forests, and eastern deciduous forests. A direct consequence of this stratification is a reduced opportunity for crown fires. Thus, repeated burning tends to reduce fire intensity, though the long-term ecological consequences of such burning may vary.

Variations in fire behavior and frequency greatly influence postfire vegetation development. In ecosystems with light to moderate intensity fires, and short return intervals, postfire species composition may be quite similar to the prefire composition, with most species being specifically adapted to either survive burning or rapidly recolonize burned sites. This is particularly true where the return interval is relatively constant. In ecosystems with longer and perhaps less predictable return intervals, postfire ecosystem response typically follows a classical species replacement series. This is clearly the case in tropical and temperate broadleaved forests.

The similarity between pre- and postfire composition is also determined in some ecosystems by fire intensity. Thus, in southeastern swamp forests, high-intensity fires may result in grass-sedge bogs, moderate-intensity fires may result in shrub bogs, and very low-intensity surface fires may alter species composition very little.

We have seen that, even within a particular physiognomic type, fire may vary in its contribution to the stability and maintenance of ecosystems. In the grasslands, for example, fire plays an essential role in preventing hardwood invasion in mesic areas. However, the absence of fire in dryer grasslands may not result in successional change. An analogous situation occurs in the savannas of the southeastern Coastal Plain.

Man's historic role in changing fire frequency and intensity is variable. The advent of man in each of the regions discussed generally resulted in an increase in fire frequency, but fire intensity increased or decreased in different vegetation types. In tropical regions, where man's association with the vegetation has been more prolonged, this alteration of ecosystems from previously existing conditions may have been more dramatic.

Recent human effects on fire regimes are even more variable. In the western coniferous forests and northern forests, fire suppression has resulted in substantial changes in fuel conditions. Although modern man further increased the number of fire starts, the area burned by fires has declined in many vegetation types. Consequently, fuels have accumulated and fire intensities have risen. In the grasslands, agriculture and dissection of the environment by roads and developments have greatly reduced fire frequencies in some areas. However, in the southeastern United States and the tropics intentional burning for silvicultural and agricultural purposes has increased fire incidence. In addition, increased fire frequencies in some parts of the southeast has been a secondary consequence of such human activities as lowering of water tables in wetland ecosystems.

Emerging from all the discussions was a clear need for further and more intensive comparative studies of fire regimes. Not only will such studies yield information on the relative impacts of differing fire regimes on ecosystem distribution and development, but these differences provide an ideal framework for asking basic ecological questions regarding the general successional consequences of the frequency and intensity of disturbances.

It was also clear from these papers, and emphasized in subsequent discussion, that we have a great deal to learn about the interaction of fire with other ecosystem processes. Kucera emphasized the interaction of fire and grazing and the difficulty inherent in trying to separate the influence of one variable from the other. The role of fire in southeastern pine forests in the control of brown-spot fungus is another example of such complex interactions. The many questions raised regarding interactions between insect epidemics, or soil characteristics, and fire regimes also indicate a need for further research.

Perhaps most significantly, the authors agreed that to determine the optimal fire regimes for a particular ecosystem we must first clearly understand what it is we wish to optimize. For example, annual and biennial prescribed fires in southeastern forests are used for specific silvicultural goals which can be quite inconsistent with the preservation of natural diversity or the reconstruction of presettlement forest conditions. In the former case the goal is to maximize extractable productivity and minimize unnecessary diversity, whereas maximization of diversity will almost necessarily result in decreased productivity of particular species. Unfortunately, in many situations the specific goals are quite nebulous. We cannot hope to successfully restore fire to ecosystems without a clear set of objectives and adequate knowledge about the various roles fire plays in ecosystems.

Simple solutions are unlikely to be found for fire management problems. As Mueller-Dombois pointed out, we must be particularly cautious about exporting our knowledge of fire and fire management techniques from one part of the world to superficially similar areas somewhere else in the world. Such a simplistic approach to fire management could lead to unwanted long-term or irreversible consequences.

The goal at the outset of this session was to enhance our understanding of fire as an ecosystem process by synthesizing existing knowledge. At best we have taken only a modest step forward in our pursuit of this goal. However, we have identified a multitude of ecosystem characteristics and processes which affect fire regimes, and we have seen how fire regimes in turn affect many of these characteristics and processes.

Improvement of our understanding of fire will, we believe, come from the study of these interactions. The papers presented here hopefully will lead us in this direction.

T. M. Bonnicksen and N. L. Christensen

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SECTION II

ADAPTATIONS OF PLANTS TO FIRE REGIMES

In the following section we probe the response of individuals and populations of organisms to fire and to habitats created by fire in time scales ranging from days to evolutionary time. By comparing the characteristics of organisms existing at sites which differ in fire frequency and intensity, we hope to distinguish between features which are responses to disturbance in a general sense to those which are specific adaptive responses to fire and various fire regimes.

If fire has been an evolutionary force, we would expect unique adaptive traits or suites of traits to be present in organisms occurring in regions with differing fire regimes, as well as within habitats occurring in a time sequence subsequent to fire within any given region. The degree to which this is true will determine how useful the study of the characteristics of individuals and populations will be for the management of ecosystems in regions where fire is an important consideration. Can we, for example, make predictions about the consequences, and, hence, potential benefits of a particular management scheme from examining the characteristics of the resident biota alone, or must we determine this empirically, through field experiment, for each site?

Harold A. Mooney



STRUCTURAL AND CHEMICAL COMPONENTS OF FLAMMABILITY

Philip W. Rundel

Department of Ecology and Evolutionary Biology
University of California

Abstract

Although fire is a natural aspect of the physical environment in many ecosystems, biotic characteristics of canopy structural form and foliage chemical characteristics may influence fire frequency and intensity. Canopy structure of plants influences the amount of energy available for combustion and the rate at which this energy is released. The chemical composition of fuels influences ignitability and the available energy content. These flammability-related characteristics may have great ecological significance to fire-adapted plants.

KEYWORDS: flammability, ether extractives, canopy structure, volatility, fire adaptations

INTRODUCTION

The hypothesis that characteristics promoting flammability are present in many plants within fire-type ecosystems has been made (Mount 1964, Jackson 1968, Mutch 1970) but unequivocal data testing this theory are lacking. If fire-adapted plants do possess an evolutionary dependence on the action of natural fires, specific suites of adaptational characteristics to promote flammability should be expected. No single index of comparative flammability is available, but a number of specific characteristics can be quantified which strongly correlate with flammability (Philpot 1977). Physical characteristics of foliage fuels and their arrangement are important determinants of the amount of energy available for combustion and the rate at which it is released (Countryman and Philpot 1970). Chemical characteristics also influence the ignition time and available heat content of fuels (Mutch 1970; Philpot 1969a, 1969b). Natural fire frequency is, of course, directly due to the occurrence of ignition events such as lightning strikes. Within a given lightning environment, however, greater potential fuel flammability may increase the statistical probability and seasonal distribution of fire.

The combustion of fuels in wildland fires represents an example of the basic process of chemical oxidation. While there has been considerable interest in the qualitative nature of what happens when fuels burn and why they burn as they do, there is a remarkably poor understanding of the quantitative aspects of these processes. In recent years there has been an increasing research into the relationships of fuel structural and chemical components of fuels to combustion characteristics. While fire is generally considered an aspect of the physical environment, the biological nature of fuel structural and chemical characteristics allows natural selection to influence suites of fire adaptive characteristics of plants in fire-type ecosystems. In this chapter, I will discuss the broad nature of structural and chemical components of flammability, review the use of these components in existing models of fire propagation, and finally discuss the hypothetical adaptive significance of such components in dominant plant species of fire-type ecosystems.

In the basic process of combustion, carbohydrates combine with oxygen to form carbon dioxide, water, and heat. Although this basic process is a simple reaction, it becomes extremely complex in woody fuels because of the nature of the variable chemical structure of the fuel. Even the molecular weights and structures of many wood components, particularly lignins, are poorly known. Generally, however, the proportions of carbon, hydrogen, and oxygen approximate multiples of $C_6 H_9 O_4$ (Brown and Davis 1973).

Three stages may be recognized in the combustion of woody fuels (Brown and Davis 1973). In the preheating or endothermic stage, the fuel absorbs heat as its temperature rises to its ignition point. The endothermic aspect of preheating results in water loss and the molecular decomposition to volatile compounds. At this stage the chemical composition of compounds which are volatile at low temperatures is of major importance in determining potential flammability. As temperatures increase, the combustion process enters one of two exothermic stages. The exothermic nature of these stages occurs as cellulosic fuels undergo pyrolysis and release heat and flammable volatiles. The temperature at which the exothermic reaction becomes self-sustaining and is difficult to determine, but most evidence indicates that this threshold occurs at approximately 300°-325°C. Once pyrolysis becomes active, ignition of flammable gases occurs readily from a pilot flame. When such ignition occurs, the combustion enters a flaming stage with burning gases. If such a pilot flame is lacking, the fuel must reach a higher temperature before spontaneous ignition can occur. Fires resulting from this buildup of heat without pilot flame ignition are termed spontaneous combustion fires. Such fires are important industrial and urban problems but rare in natural environments. The third stage of combustion, without flaming gases, occurs as residual charcoal is burned in what is termed glowing combustion. Oxidation takes place at the fuel surface combining carbon monoxide, formed as an intermediate product, with oxygen to release CO_2 . The relative amount of heat energy released in the flaming stage compared with the glowing stage varies considerably between fuels. Generally, however, the glowing stage produces more total heat of combustion but at a slower rate than the flaming stage (Brown and Davis 1973). For both of these stages the structural and chemical components of the fuel are extremely important in determining variable combustion behavior.

STRUCTURAL COMPONENTS OF FLAMMABILITY

No single index of structural characteristics of plant canopies or litter layers relating to relative flammability is available, but a number of specific structural traits which strongly correlate with flammability can be quantified. These traits, including fuel loading, particle density, fuel surface-to-volume ratio, and fuel porosity, have significance because of their influence on ignition probability, rate of fire spread, and/or fire intensity.

Fuel loading, measured as the dry weight of fuel per unit of canopy area, provides a measure of the amount of fuel available to burn. With all other conditions being equal, the amount of heat provided by a fire would be a function of this fuel loading. Used alone, however, fuel loading is a poor predictor of fire behavior. Variations in other structural characteristics as well as moisture content and chemical composition are all significant in determining the amount and rate of energy release through pyrolysis.

Particle density (specific gravity), measured as weight per unit volume of fuel, influences flammability through its effect on thermal conductivity and thereby time to ignition. Fons (1946, 1950) has shown that rate of spread in experimental fires decreases with increased fuel density. The type of ignition (i.e., whether of the pilot-flame or spontaneous type) occurring in a fuel is also a function of particle density (Brown 1970a). In conifers, density of wood varies considerably among species and to a smaller degree among geographically separated populations of the same species. Within the same species, however, densities of small diameter branches are relatively constant (Ryan and Pickford 1978; Brown 1974).

Fuel surface-to-volume ratio commonly symbolized as σ , provides an important index of both flammability and combustion, since heat transfer by radiation, conduction, and convection are all a function of surface area. Therefore, the greater the surface area in relation to volume, the more rapid the transfer of heat to the fuel interior and the more rapid the combustion of the fuel (Countryman and Philpot 1970). This effect occurs both directly through temperature change and indirectly through change in the moisture content of the fuel (Fons 1950; King and Linton 1963). Laboratory experiments have shown that rate of fire spread increased linearly with increased S/V ratio while ignition time varies inversely (Curry and Fons 1938; Fons 1946, 1950; Rothermel and Anderson 1966).

Fuel surface-to-volume ratios vary greatly in different fuel types. Since many fire-type plant communities contain fine foliage with high values of σ , comparative determinations of σ provide one measure of potential structural flammability (table 1). Evergreen conifers have values ranging from 54 to 99 $\text{cm}^2\text{cm}^{-3}$, while deciduous Larix has a much higher ratio of 184. Grasses are highly flammable components of many communities and the high values of σ for leaves of this group range from 189-380 $\text{cm}^2\text{cm}^{-3}$. Grass stems are comparable to conifer needles (table 1). Leaves of evergreen chaparral shrubs and evergreen trees also have comparable values of σ . Alectoria jubata, a highly flammable lichen occurring in dense quantities on Picea in taiga ecosystems, has a fine branch structure and resulting remarkable σ value of 632 $\text{cm}^2\text{cm}^{-3}$ (Brown 1970b). Montgomery and Cheo (1971) studied the delay time for spontaneous ignition in a 750°C muffle furnace for leaves of 33 species of native chaparral shrubs and introduced shrubs in the Los Angeles State and County Arboretum and found that ignition times varied inversely with the log of σ and directly with leaf thickness.

TABLE 1.--Ratios of surface area to volume (σ) for foliage fuels.
For grasses, values for leaves/stalks are shown. Data
from Brown (1970b) and Montgomery and Cheo (1971)

	$\sigma(\text{cm}^2 \text{cm}^{-3})$
<hr/>	
Needles	
<u>Picea engelmannii</u>	54.2
<u>Pinus ponderosa</u>	57.6
<u>Pinus contorta</u>	64.7
<u>Pseudotsuga menziesii</u>	69.1
<u>Abies grandis</u>	72.9
<u>Pinus monticola</u>	90.5
<u>Tsuga heterophylla</u>	99.8
<u>Larix occidentalis</u>	184.0
Grass	
<u>Calamagrostis rubescens</u>	240/51.8
<u>Festuca idahoensis</u>	190/68.6
<u>Agropyron spicatum</u>	271/44.6
<u>Taeniantherum asperum</u>	380/58.5
<u>Bromus tectorum</u>	189/75.8
<u>Bambusa multiplex</u>	363.2
Evergreen Shrubs	
<u>Rhus ovata</u>	71.7
<u>Heteromeles arbutifolia</u>	80.0
<u>Eriodictyon trichocalyx</u>	76.0
<u>Prunus ilicifolia</u>	133.2
<u>Rhamnus crocea</u>	127.0
<u>Rhus laurina</u>	126.0
<u>Quercus dumosa</u>	126.0
Evergreen Trees	
<u>Magnolia grandiflora</u>	84.7
<u>Eucalyptus globulus</u>	94.7
<u>Eucalyptus obliqua</u>	61.8
Lichen	
<u>Alecoria jubata</u>	632.4

Fuel bed porosity, the ratio of canopy volume to fuel volume, provides another structural component which is positively correlated with rate of spread in fires (Rothermel and Anderson 1966). Increased porosity allows both greater convective heat transfer and greater oxygen circulation within a fuel canopy and thus strongly influences fire spread. Numerous studies have shown that measures of burning rate increase with increasing porosity up to a threshold point (Curry and Fons 1940; Gross 1962; Byran and others 1964; Anderson and others 1966). If spacing becomes too great, unburned fuel particles may not receive sufficient heat for ignition. Thus low values of fire intensity and rate of spread occur at the two extremes of porosity--loose and dense. At the loose end of this spectrum, low intensity and poor rate of spread are attributed to inefficient heat transfer between fuel particles and to lack of fuel biomass. In dense beds, low air-to-fuel ratio and poor penetration of heat beyond surface layers of the fuel can cause this result. Several other measures of fuel bed porosity have been described (Brown 1970a). These are the ratio of void volumes in a fuel bed to surface area of fuel, the average distance between fuel particles, and the bulk density of the fuel bed (weight per unit volume of fuel bed). The latter measure of bulk density is only a crude estimate of porosity since it does not consider the specific gravity of the fuel but it has the advantage of being relatively easy to measure. Brown (1970a) has shown a highly significant correlation between all three of these measures of porosity for ponderosa pine litter and Bromus tectorum (cheatgrass) canopies.

An integrated dimensionless indicator of fuel structural flammability, a product of fuel S/V ratio σ and ratio of void volume to fuel surface area λ , has been used in fire behavior modeling (Rothermel and Anderson 1966). Both particle size and fuel bed porosity are incorporated in $\sigma\lambda$. Past studies with this index, however, have dealt with only a single fuel particle size. More experimental studies using a weighted index of different fuel size classes are needed to assess the significance of this integrated measure.

Because of the importance of structural components of flammability in herbaceous and woody ground fuels, the USDA Forest Service has given considerable attention to sampling the structure of fuel. Standardized techniques have been developed for inventorying downed woody material (Brown 1970a, 1974; Brown and Roussopoulos 1974). Albini (1976b) assembled data on comparative structural characteristics for selected fuel complexes (table 2). Table 2 is an adaptation of these data.

The significance of fuel moisture in influencing flammability is strongly dependent on a fuel structural characteristic which relates to heat transfer. High moisture content of leaves has been shown to significantly reduce relative flammability (Olsen 1960, Montgomery and Cheo 1971, Countryman 1974). Of more structural significance, however, is the relative capacity of fine fuels to rapidly change moisture content. This characteristic may determine if combustion will occur. Equilibrium moisture contents of such fuels may be calculated from temperature and relative humidity data and serve as important indexes of flammability. Fosberg and Schroeder (1971) have developed models to predict adjusted fuel moisture contents for mixtures of fine dead and living fuels.

Biological variation in the timelag for fuel moisture content to equilibrate in morphologically similar conifer needles is very significant varying from 4 to 21 hours for different species of pine (King and Linton 1963, Simard 1968, Van Wagner 1969). After 1 year of weathering all needles equilibrate much more rapidly, apparently due to a combination of structural and chemical changes (Anderson and others 1978).

TABLE 2.--Comparative structural characteristics for selected fuel complexes. Values are given for typical surface to volume ratio and fuel loading for each type of fuel. Moisture of extinction is the maximum fuel moisture content which will allow combustion to occur. Data adapted from Albini (1976b)

Fuel complex	Surface to volume ratio/fuel loading				Fuel depth (cm)	Moisture of extinction (% of dead fuel)
	$\sigma \text{ (cm}^2\text{cm}^{-3})/(\text{gxm}^{-2}) \text{ or (g/m}^2\text{)}$			Live fuel foliage		
	Dead fuel (dia. in cm)					
	<u><0.6</u>	<u>0.6-2.5</u>	<u>2.5-7.6</u>			
Grass and grass dominated						
Short grass	115/165				30	12
Timber understory	98/447	4/224	1/112	49/112	30	15
Tall grass	49/671				75	25
Chaparral and shrubfields						
Chaparral	66/1119	4/895	1/448	49/1119	180	20
Brush	66/224	4/112		49/448	60	20
Dormant brush/hardwood slash	57/336	4/559	1/448		75	25
Southern rough	57/253	4/418	1/336	51/83	75	40
Timber litter						
Closed timber litter	66/336	4/224	1/559		6	30
Hardwood litter	2/652	4/92	1/34		6	25
Timber (litter and understory)	66/671	4/448	1/1119	49/448	30	25
Logging slash						
Light slash	49/336	4/1007	1/1231		30	15
Medium slash	49/895	4/3132	1/3692		70	20
Heavy slash	49/1566	4/5146	1/6265		90	25

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Until the past 15 years studies of wildfire behavior and flammability concentrated heavily on investigations of the structure characteristics and moisture relations of fuels which influenced their flammability. While structural and fuel moisture components of flammability are extremely important, it is clear that pyrolysis may be influenced by both inorganic and organic constituents of fuels. These components influence the effective heat content of combustible gases released by pyrolysis and thus the energy available to maintain ignition of additional fuel elements. This effective heat content is only a portion of the total heat of combustion. In addition, the nature of chemical components determines the temperature dependence of the release of combustible volatiles.

Cellulosic and Inorganic Components

Typical cellulosic fuels such as wood are composed of structural components of approximately 42% cellulose, 25% hemicellulose, and 33% lignin (Philpot 1970). The thermal decomposition characteristics of these three components are shown in figure 1. Acid lignin is relatively stable thermally compared with cellulose and hemicellulose, losing only about 30% of its initial dry weight at 400°C. This thermal stability makes lignins much less important than carbohydrate products for fire problems. In addition, many of the pyrolytic products of lignin have a much higher molecular weight and are less volatile than products from carbohydrates (Kitao and Watanabe 1967). Cellulose is thermally stable until just over 300°C when it undergoes rapid pyrolysis. Hemicelluloses such as xylan begin to decompose at lower temperatures than cellulose although they produce the same general type of volatiles (Shafizadeh and others 1969). Thus cellulose and hemicellulose components of woody fuels are much more significant than lignin content in the production flammable volatiles.

Broido (1966) demonstrated that the net pyrolytic response of pure cellulosic fuel could be altered dramatically by the presence of minerals in concentrations as low as 0.15%. The addition of 1.5% potassium bicarbonate caused thermal decomposition to begin at a lower temperature but decreased the maximum rate and magnitude of volatilization. Similar results showing a relationship between inorganic components and both pyrolysis and combustion were shown in other studies (Broido and Nelson 1964; Tang and Neill 1964; Waisel and Friedman 1966). Mutch and Philpot (1970) determined that the silica fraction should be discounted when relating mineral content to pyrolysis and ignition in fuels. They recommend the use of silica-free ash content in combustion studies.

The relationship of the range of pyrolytic properties of wildland fuels to silica-free ash content was clearly demonstrated by Philpot (1970). Combustion data for cellulose and 16 wildland fuels are shown in table 3 for ash contents, % volatilization over the temperature range of 175°C-350°C, the maximum rate of volatilization, and organic residue at 400°C. The greatest changes in pyrolytic properties occurred in fuels with silica-free ash contents below 5.2%. In the four halophytic species with ash content above 12%, effects on pyrolysis were not proportionally increased. It is likely that the high concentration of sodium and potassium, and possibly other anionic components is less important in influencing pyrolytic properties (Philpot 1970).

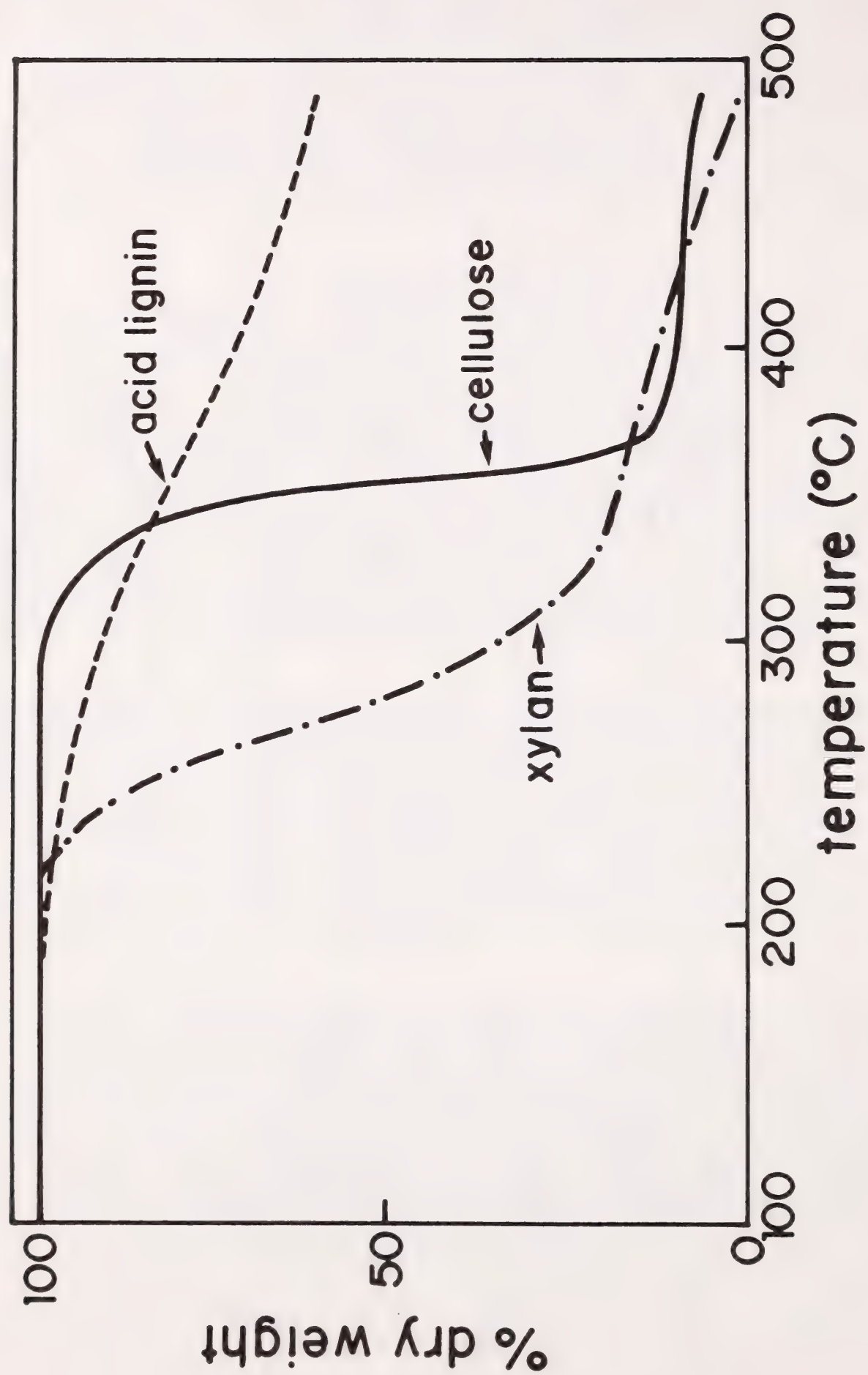


Figure 1.--Thermal decomposition characteristics of acid lignin, cellulose, and xylan (hemicellulose).
Adapted from Philpot (1970)

Table 3.--Mineral content and volatilization characteristics of selected plant material. Data from Philpot (1970)

	Plant part	Silica-free ash (%)	Total ash (%)	Volatilization 175° - 350° C (%)	Max Vol rate (µg C)*	Organic residue at 400° C (%)
Cellulose	--	0.01	0.01	94	232	5
<u>Pseudotsuga menziesii</u>	wood	0.11	0.11	71	84	26
<u>Betula sp.</u>	wood	0.18	0.18	79	84	19
<u>Pinus ponderosa</u>	wood	0.22	0.22	73	84	23
<u>Populus sp.</u>	wood	0.36	0.36	70	72	19
<u>Bromus tectorum</u>	leaves	1.04	5.27	73	68	26
<u>Taeniatherum asperum</u>	leaves	1.17	16.02	69	65	33
<u>Pinus ponderosa</u>	needles	1.55	3.87	61	48	35
<u>Adenostoma fasciculatum</u>	stems	1.75	2.19	60	50	34
<u>Pinus monticola</u>	needles	2.54	3.34	59	44	38
<u>Adenostoma fasciculatum</u>	leaves	3.33	3.63	55	48	38
<u>Populus tremuloides</u>	leaves	5.24	5.24	55	46	42
<u>Atriplex canescens</u>	leaves	12.29	12.89	56	45	44
<u>Tamarix aphylla</u>	leaves	14.53	16.59	50	34	50
<u>Atriplex polycarpa</u>	leaves	14.83	15.39	58	47	47
<u>Atriplex lentiformis</u>						
var. <u>breweri</u>	leaves	18.63	19.26	57	48	48
<u>Atriplex gardneri</u>	leaves	23.57	26.78	55	49	56

*10 mg samples

Phosphorus content of fuels frequently shows an inverse relationship to flammability. Philpot (1970) found that maximum rate of volatilization was highly correlated with phosphorus plus calcium contents of wildland fuels. Phosphorus content of foliage has been shown to relate to fire rate of spread in Arizona oak chaparral with increased rates of spread below a threshold concentration of phosphorus (Lindenmuth and Davis 1973). The importance of phosphates to flammability has also been discussed by Countryman and Philpot (1970), Rothermel (1976), and Granzow (1978).

The effect of inorganic salts in affecting pyrolytic reactions in cellulosic fuels is not clearly understood. The general response, however, is brought about by altering pathways of pyrolysis so that more char and fewer flammable volatiles are formed. As a result there is a reduction in the overall intensity of combustion. Frequently there is also an inhibition of the glowing combustion of char and thus further reduction of heat production (Rothermel and Philpot 1975). The effects of such inorganic salts are the basis of action for many chemical fire retardants. Both natural inorganic components and artificial retardants have the overall effect of decreasing maximum rates of volatilization, increasing char residue, and initiating pyrolysis at lower temperatures (Philpot 1970, Tang 1967, Tang and Eickner 1967). Numerous laboratory tests with ammonium polyphosphates, perhaps the most widely used type of chemical fire retardant today, have shown that the effectiveness of solutions is related to the amount of active phosphate available to alter pyrolysis and combustion reactions (George and others 1977). Impurities such as calcium, magnesium, and iron in these solutions may chemically bind available phosphorus and reduce the fire retardant effectiveness.

Biochemical Components

Two fundamental properties of any fuels in fire studies are the temperature at which ignition occurs and the available energy released from the fuel in the combustion process. Most models of fire behavior compute reaction intensity of fires as a function of the heat of combustion (calories per gram of fuel) and the mass loss rate (grams per m² of surface) with particular attention to structural characteristics of fuels, fuel moisture, and fuel mineral contents (Rothermel 1972). However, these models assume heat of combustion to be the low heat value obtained from oxygen bomb calorimeter studies, and therefore fail to distinguish between effective heat content available as combustible volatiles and energy present in the char (Rothermel 1976). Since a significant percentage of the combustible volatiles of plant tissues may be in the form of high-energy terpenes, fats, oils, and waxes, the flammability of individual tissues may vary considerably despite a small overall range of heat contents of total fuel biomass (Philpot 1969). These high-energy energy compounds are extremely significant in flammability because they commonly undergo combustion at relatively low temperatures without prior complex pyrolytic reactions and are frequently deposited on or near the surface of plant parts, particularly leaves. Much of the extreme flammability attributed to specific fuels appears to be due to the relatively high concentrations of high-energy compounds in foliage tissue. Commonly, live chaparral fuels with moderate or high ether extractive contents will burn at moisture contents of 100% or more, while dead fuels will not burn well above 20 to 30% fuel moisture (Rothermel 1976). Leaves of Psidium guajava (guava) killed by herbicide treatment burn much less readily than leaves that die naturally. Philpot and Mutch (1968) attributed this change to an 18% reduction in ether extractives associated with the herbicide treatment. Philpot (1969b) found that the maximum burning rate of leaves of Populus tremuloides was directly proportional to their extractive content. Essential oils (terpenes) of eucalyptus leaves promote flammability by increasing the evolution of heat in the early stages of combustion (Pompe and Vines 1966). The rate of heat release is increased significantly in relatively nonflammable foliage by the addition of such oils (King and Vines 1969). Philpot (1969a) found a direct relationship between total heat content of Adenostoma fasciculatum and ether extractive content. Montgomery (1976) found significant correlations of combustion characteristics in leaves of 16 species of Mediterranean

climate shrubs with ether extractive contents. Ignition time-delay varied inversely with extractive content, while flame height and brightness were directly related to the log of extractive content.

Although ether extractive constituents of flammable species have yet to be fully characterized, preliminary investigations in our phytochemical laboratory indicate that the ether extractives consist of numerous secondary constituents, including methylated flavonoids, sesquiterpenes, waxes, triterpenes, and esterified phenolics. External leaf dippings also show the presence of volatile monoterpenes, amines and possibly prussic acid. In many cases these external compounds are low molecular compounds (75-300 mw), which are highly flammable under high temperature conditions. The combustion products of monoterpenes and many of the amines are thermodynamically unstable, as are many other volatiles. In an oxygen atmosphere, they are susceptible to flaming combustion if ignited. Unlike cellulose and other polymers which must be decomposed before combustion can occur, small molecular-weight compounds volatilize without decomposition (Rothermel 1976). In the case of polymeric materials, vaporization and combustion are preceded by decomposition of the polymer into small molecular-weight fragments (Granzow 1978).

While ether extractive components such as terpenes provide a large component of low temperature volatiles, a number of more polar benzene-ethanol extractives are volatile at temperatures below 300°C. These extractives may include certain resins, sugars, and other readily soluble compounds. Shafizadeh and others (1977) have investigated the role of both ether and benzene-ethanol extractives in determining the volatilization of wildland fuels. Ether extractives in the foliage of the six species they studied ranged from 1.9 to 16.8%, while the benzene-ethanol extractives ranged from 11.2 to 32.8% (table 4). The total extractive content of Ilex glabra (gallberry) is a remarkable 44.6% of the foliage dry weight. Analyses of C and H in these samples, which provide an index of heat combustion and flammability, show that the ether extractives have a significantly higher C and H content than the benzene-ethanol extractives and nonextractives (table 4). As a result, these ether extractives contribute very heavily to the effective heat content and total heat of combustion (Susott and others 1975, Shafizadeh and others 1977). Thermal analyses of the temperature dependence of the production of combustible volatiles were carried out by Shafizadeh and others (1977) on unextracted and extracted samples of foliage of six species. Over the temperature range of 100°-500°C, the majority of combustion gases in Pseudotsuga menziesii, Pinus ponderosa, Populus tremuloides, Ilex glabra, and Arctostaphylos patula are derived from ether and benzene-ethanol extractives. Between the two extractive components, the ether extractives generally contribute the larger amount of combustible gases despite their lower content (table 4) because of their complete volatilization and their higher heat of combustion. In Senecio repens, which has a comparatively low total extractive content of 13%, most of the combustible gases are formed from pyrolysis of nonextractive components, presumably cellulosic material (Shafizadeh and others 1977).

TABLE 4.--Extractive contents and carbon and hydrogen contents of foliage of six ever-green species. Data from Shafizadeh and others (1977)

	Ether extractives			Benzene-ethanol extractives			Nonextractives		
	%	C(%)	H(%)	%	C(%)	H(%)	%	C(%)	H(%)
<u>Pseudotsuga menziesii</u>	11.2	59.8	9.0	19.1	55.9	8.1	69.7	48.3	6.0
<u>Pinus ponderosa</u>	11.8	61.3	8.6	19.0	47.1	7.3	69.2	47.8	6.4
<u>Populus tremuloides</u>	16.8	73.3	11.8	19.8	47.4	6.8	63.4	44.3	5.8
<u>Ilex glabra</u>	11.8	76.5	11.4	32.8	50.8	6.4	55.4	49.4	6.7
<u>Arctostaphylos patula</u>	9.5	76.8	10.9	16.3	46.2	6.5	74.2	49.4	6.4
<u>Serenoa repens</u>	1.9	70.4	10.4	11.2			86.9	48.3	5.8

Thermal analyses of the ether and benzene-ethanol extractives of foliage of Pinus ponderosa and Arctostaphylos patula (fig. 2) show that virtual complete volatilization of ether extractives occurs over the temperature range of 100^o-500^oC (Shafizadeh and others 1977). In Pinus ponderosa there is a gradual volatilization over the temperature range with a low peak at about 270^oC. In Arctostaphylos there is slow volatilization at low temperatures followed by a sharp peak centering at 300^oC. Benzene-ethanol extractives behave quite differently, decomposing gradually at low temperatures of 200^o-300^oC. The compounds contained in ether extractives may play a significant role in both the initiation of combustion at low temperatures and the increase in fire intensity at higher temperatures due to their volatile characteristics and high energy content. Cellulose does not undergo pyrolysis below 300^oC and thus contributes to combustion only at high temperatures.

The heat content of the ether extractive components of fuels far exceeds that of other components. Caloric values of unextracted foliage of Mediterranean sclerophyll shrubs of California range from 17.6 to 21.8 kJ g⁻¹ (4200 to 5200 cal g⁻¹) (Rundel, unpublished data). Philpot (1969a) found that the heat content of the ether extractive component of leaves of Adenostoma fasciculatum ranged as high as 40.19 kJ g⁻¹ (9600 cal g⁻¹) and stem ether extractives ranged up to 56.94 kJ g⁻¹ (13600 cal g⁻¹). Simple fire models used to predict the heat of combustion of flammable volatiles in fuels use generalized figures of 16.1 kJ g⁻¹ (3850 cal g⁻¹) of cellulose, 24.5 kJ g⁻¹ (5860 cal g⁻¹) of lignin, and 32.3 kJ g⁻¹ (7720 cal g⁻¹) of ether extractives (Susott and others 1975, Rothermel 1976).

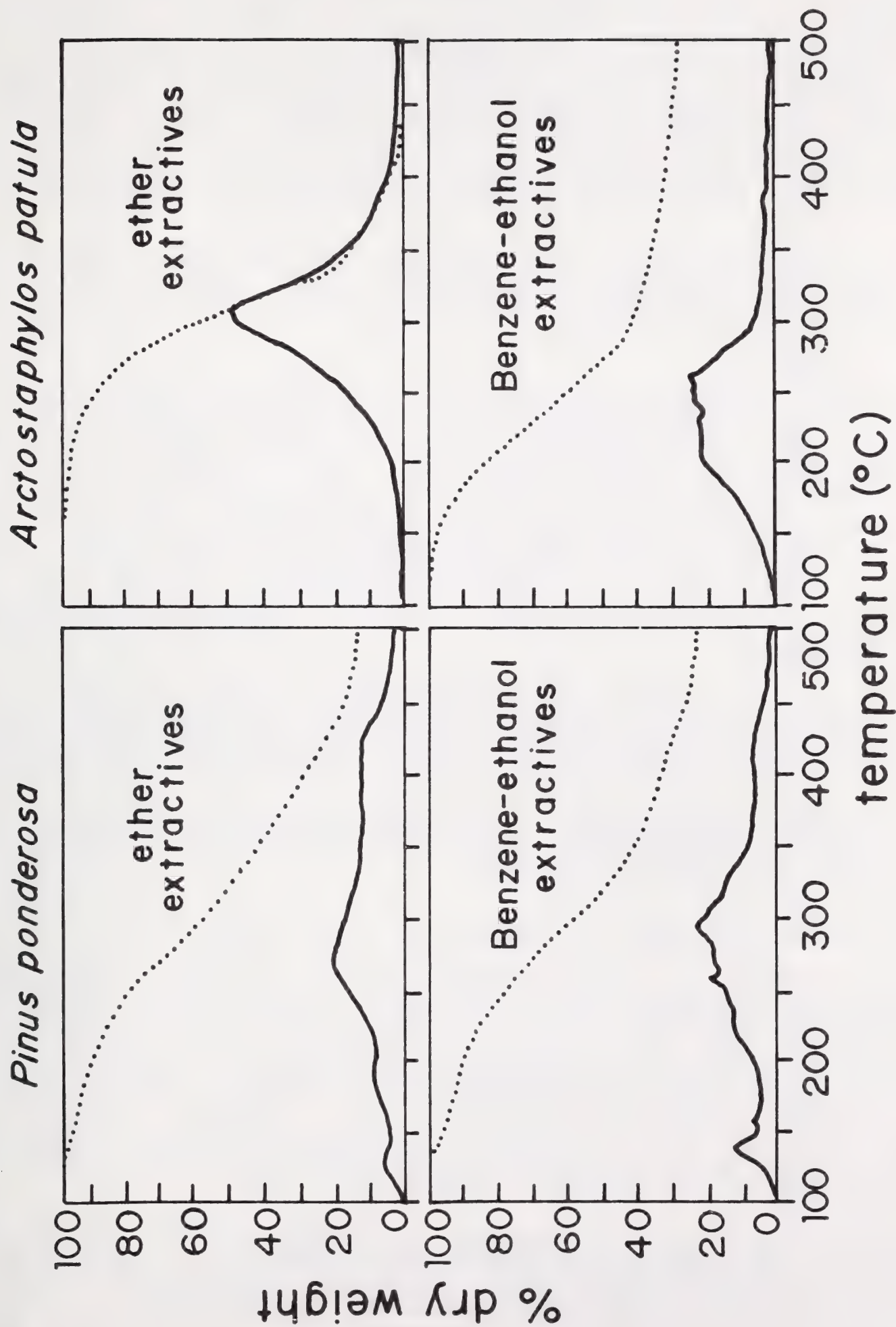


Figure 2.--Thermal decomposition characteristics of ether extractives and benzine alcohol extractives of *Pinus ponderosa* and *Arctostaphylos patula*. Both total weight loss (solid line) and weight loss at a given temperature (dotted line) are indicated. Adapted from Shafizadeh and others (1977).

Only a few studies have looked at the seasonal variations of ether extractive components and energy contents of fuels. Richards (1940) found a doubling in extractives in Ceanothus velutinus from 5.2% in June to 11.5% in September, with corresponding increases of 20% in energy content. Similar patterns of seasonal change for extractives and energy content have been found for rangeland shrubs in Colorado, including Purshia tridentata, Cercocarpus betuloides, and Artemisia tridentata (Dietz and others 1962; Short and others 1966). Energy values increased 9.0, 1.0, and 3.6% respectively for midsummer to fall, while ether extractive content changed 61, 42, and 6%. The physiological significance of this seasonal pattern was not investigated, however, and any possible role of ether extractives in influencing flammability in these species is conjectural.

Ether extractive concentrations in Pinus clausa reach their highest level of 12 to 14% in early March when needle water content is at its lowest. The time period is correlated with the period of greatest acreage burned over the course of the year (Hough 1973).

Philpot (1969a) showed that concentrations of ether extractives in Adenostoma fasciculatum also vary considerably seasonally. Leaf contents ranged from a low of 8.5% in spring to 12% in fall, while stems ranged from a low of 4.3% to a high of 8.9% (fig. 3). The fall increase in extractives, however, does not correlate well with the frequency of occurrence of lightning fires in the mountains of southern California (fig. 3). Philpot hypothesized that the spring dip in extractive content was due to a mobilization of compounds associated with stem elongation and new leaf growth. Variable relationships of energy values and extractive contents, however, indicated that a significant compositional change was occurring seasonally in the compounds making up the extractives. Very little is known about the nature of individual ether extractive compounds in Adenostoma.

Simple empirical models have been developed to predict the heat of combustion of flammable volatiles as a function of relative proportions of cellulose, lignin, ether extractives, and inorganic minerals in fuels (Susott and others 1975, Rothermel 1976). The relationship of these models to field behavior in combustion has not been tested.

These models have inherent defects in that they ignore possible variations of heat content in the ether extractive components and fail to consider the significance of benzene-ethanol extractives in combustion.

THE ROLE OF STRUCTURAL AND CHEMICAL DATA IN FIRE BEHAVIOR MODELS

A variety of mathematical models of varying scope and complexity have been developed to estimate wildfire behavior (see summary review in Albini 1976b). While the majority of these are highly theoretical, many have been designed to allow forest and rangeland managers use of a uniform method of predicting both rate of spread and fire intensity in the field. Typically these models relate physical and chemical properties of fuels to specific fire behavior such as forward rate of spread, fire intensity, flame length, and burning time. Environmental factors of slope angle, windspeed, and fuel moisture content are used in these models. Mathematical models of heat required for ignition of fuels are also available (Stockstad 1975; 1976).

While data to test theoretical fire models are difficult to obtain because of the unpredictable nature of fires, current models provide useful predictive information on fire behavior (Deeming and others 1977). Nevertheless, calculations may be made of theoretical values for reaction intensity and heat required for ignition using field-collected data on structural and chemical characteristics of individual fuels. Rothermel and Philpot (1973) used such models to predict changes in Adenostoma chaparral flammability.

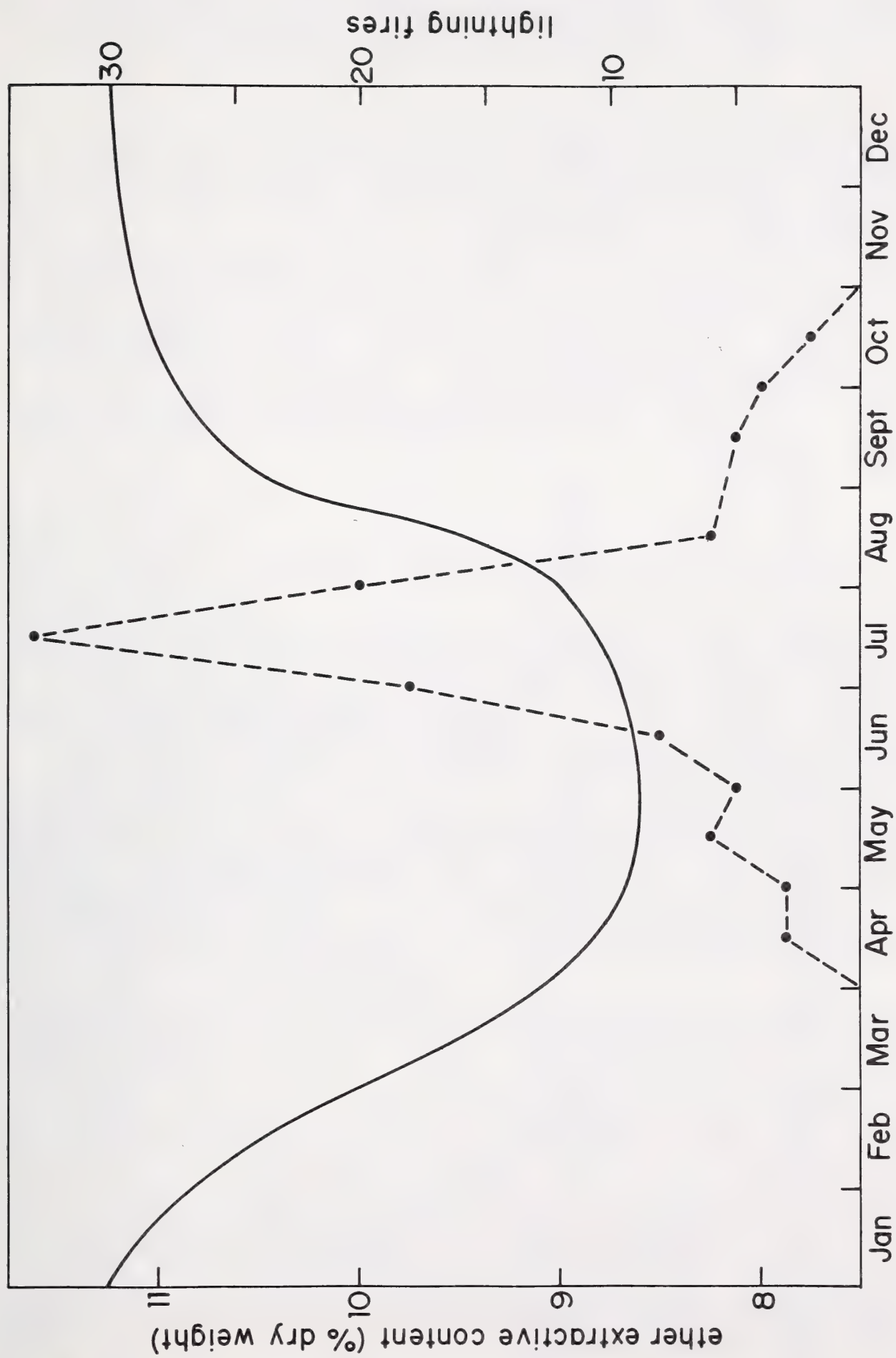


Figure 3.--Ether extractive content of *Adenostoma fasciculatum* (solid line) and number of lightning strikes (dashed line) over an annual cycle. Data from Philpot (1969a) and Keeley (1977).

These models assume a continuous and homogeneous canopy structure for a monoculture of each fuel type, an assumption which is obviously not ecologically realistic. In addition, they do not adequately consider the potential chemical variability of ether extractive components. Despite these drawbacks, however, the existing models provide valuable data for predicting fire behavior. Theoretical fire characteristics for generalized fuel types utilized in the 1978 National Fire-Danger Rating System are shown in table 5.

The most comprehensive fire spread rate model for wildland fuels is that of Rothermel (1972) which has been further adapted by Albini (1976a, 1976b) into a utilitarian model widely used in the National Fire-Danger Rating System (Deeming and others 1977). The basic structure of this model is an expression of the conservation of energy in combustion (Frandsen 1971). It assumes that fire spreads by a sequence of ignitions beginning with fine fuels from the top to the bottom of the canopy. In a fuel of constant chemical structure, the fire burns at a rate determined by the size and arrangement of fuel particles, thereby providing heat energy to ignite adjacent fuels. Details of the model and the basis for many parameters used can be found in Rothermel (1972) and Rothermel and Anderson (1966). It has been subject to field verification in logging slash fires (Brown 1972) and grass fires (Sneeuwjagt 1974). Lindenmuth and Davis (1973) used the same inputs weighted differently to model fire spread in Arizona oak chaparral.

EVOLUTIONARY ASPECTS OF FLAMMABILITY

Flammability and Patterns of Fire Adaptation

The relationship of structural and chemical components of fuels to patterns of fire adaptation has been described by St. John (1976). He distinguishes three responses of fire-adapted plants to fire: survival with essentially no damage (mature-lives strategy), death of the plant in the fire (mature-dies strategy), and destruction of foliage with rapid regeneration (resprout strategy). Plants with the "mature-lives" strategy share several types of structural adaptations to maximize the probability of their surviving a fire. These include, first, thick bark to insulate the cambium from heat of a fire (Martin 1963, Hare 1965, Gill and Ashton 1968, Vines 1968) and, secondly, relative tall stature in their communities to minimize the possibility of the spread of ground fires into the canopy. A third characteristic is the presence of relatively long needles in conifers or comparable leaf structures in other species which allow a buildup of dry well-aerated mats of litter. This litter promotes ground fires which are important in promoting reproductive success of these "mature-lives" species.

"Mature-die" species in St. John's system typically produce dense, even-aged stands which have the structural characteristic of senescing relatively contemporaneously to promote severe but infrequent fires. Such a fire severity results in dense reproduction, survival, and ecological success of "mature-die" species. While it has not been investigated, it could be hypothesized that the chemical components of flammability would be relatively insignificant in this fire-adapted group since they would not promote infrequent fire. In the resprout strategy, both structural and chemical components appear to be common in promoting flammability at frequent intervals independent of stand age or health. One common structural component increasing flammability in such species is the retention of fine dead fuels in the crown as noted in Xanthorrhoea australis (Specht and others 1958), Eucalyptus macrorhyncha (Moore and Keratis 1971), and Adenostoma fasciculatum (Rothermel and Philpot 1973, Rundel and Parsons 1979). High contents of high energy ether extractives are a typical chemical component of flammability in resprout species.

TABLE 5.--Theoretical fire characteristics for generalized fuel types based on fuel models of the 1978 National Fire-Danger Rating System. Fuel moisture conditions of four dead fuel size classes and two living fuel classes are estimated for each climatic type. Wind conditions are calculated for 32 km h⁻¹ at 6 m height with a 0 to 25% slope. Data adapted from Deeming and others (1977).

Fuel model	Available energy	Theoretical spread rate	Flame length
	(cal cm ⁻²)	(cm sec ⁻¹)	(cm)
I. Arid and semiarid desert and grassland			
annual grasses and forbs	27	1122	311
sagebrush-grass	142	262	354
II. Shrubland, eastern Great Basin, open conifer forest			
annual grasses	20	963	271
perennial grasses	41	590	292
Alaska tundra	163	47	171
sageland-grass	122	232	314
intermountain brush	217	106	283
chaparral	468	191	524
open timber-grass	136	89	210
III. Subhumid grasslands, hardwood forests, and dense mountain conifer forests			
perennial grass	20	350	174
sawgrass	170	329	421
pocosin	468	195	530
western, long-needled conifer	244	31	168
southern pine plantation	196	28	146
southern pine/shrubland	326	134	381
short-needled conifers-healthy	234	16	119
short-needled conifers-overmature	414	59	290
Alaskan black spruce	380	116	378
hardwoods-winter	183	57	198
hardwoods-summer	122	12	79
light slash	461	45	271
medium slash	1363	87	600
heavy slash	2326	128	917
IV. Pacific Coast temperate rain forest			
short-needled conifers-healthy	190	14	107
short-needled conifers-overmature	353	53	259
light slash	407	41	244
medium slash	1214	79	543
heavy slash	2062	116	829

Flammability and Nutrient Cycling

Natural fire provides a critically important pathway for decomposition and cycling of nutrients in Mediterranean-climate ecosystems with low nutrient availability. In these areas natural selection has operated to maintain flammable shrub structures and chemistries which favor relatively efficient use of this fire-cycling. This hypothesis suggests that dominant shrubs in the chaparral of California (low soil fertility) should have evolved a pattern of more flammable characteristics than morphologically similar shrubs in the matorral of central Chile (moderate fertility). Such a pattern appears to exist.

Structural characteristics of dominant shrub species from California chaparral and Chilean matorral indicate that California shrub canopy architecture is significantly more flammable than that of Chilean species for several characteristics (Mooney and others 1977). Fuel loading in California is more than twice that in Chile, but this factor may relate to the past history of human activities in central Chile. More significant, however, are the higher percentages of fine-stem fuels in California. The extremely high surface area in Adenostoma fasciculatum is particularly notable.

If the hypothesis of chemical adaptation of flammability in California shrubs in relation to Chilean shrubs is correct, the heat of combustion of the flammable volatiles should show broad patterns of difference between the two regions. California foliage would be expected to have higher heat-of-combustion values for leaf than stem tissue due to storage of volatile high-energy ether extractives. In comparison to Chilean shrubs, the heat of combustion of flammable volatiles should be much higher, particularly in leaf tissue. Calculations of thermodynamic data of fuels, characteristic of foliage from these two regions, shown in table 6, strongly support this hypothesis. The mean heat of combustion of volatiles in California leaves is 9.80 kJ g^{-1} released per gram of fuel, nearly 40% higher than the Chilean mean value. Stem values are nearly 20% higher.

Individual chemical characteristics relating to flammability of foliage further support the greater potential flammability of California shrubs (table 7). Although leaf caloric values have a relatively small range of variation, the mean heat content of California shrubs is significantly higher than that of Chilean shrubs. Adenostoma is notably high among all the species tested. Greater differences between the two regions can be seen in the leaf content of ether extractives. Four California species have a mean content of 6.25 against only 1.87 in the Chilean species. Total shrub ether extractives, based on analyses of 3-year-old stem tissue, shows a similar but smaller pattern of difference. Mineral content and total phosphorus content are not significantly different in the two regions.

TABLE 6.--Calculated characteristics for second-year leaves and stems of dominant California chaparral and Chilean matorral shrubs. Heat of combustion values are corrected to 400°C. Data calculated from models of Susott and others (1975) and Rothermel (1976)

	H-fuel	Char	H-volatiles
	(kJ g ⁻¹)	(%)	(kJ released g ⁻¹ fuel)
California leaves			
<u>Adenostoma fasciculatum</u>	20.38	31.7	11.11
<u>Arctostaphylos glauca</u>	20.75	35.7	10.32
<u>Rhus ovata</u>	18.46	31.0	9.39
<u>Ceanothus greggii</u>	18.86	35.9	8.38
Mean	19.61	33.5	9.80
California stems			
<u>Adenostoma fasciculatum</u>	20.21	33.2	9.80
<u>Arctostaphylos glauca</u>	18.62	32.3	9.17
<u>Rhus ovata</u>	18.88	36.1	8.33
<u>Ceanothus greggii</u>	18.88	34.6	8.78
Mean	19.14	34.0	9.20
Chile leaves			
<u>Lithraea caustica</u>	18.32	34.8	8.13
<u>Kageneckia oblonga</u>	17.54	33.9	7.64
<u>Cryptocarya alba</u>	18.58	38.1	7.15
<u>Colliguaya odorifera</u>	18.77	39.0	7.38
<u>Satureja gilliesii</u>	18.35	40.3	6.57
<u>Quillaja saponaria</u>	16.53	36.7	5.82
Mean	18.00	37.1	7.17
Chile stems			
<u>Lithraea caustica</u>	18.42	37.9	7.36
<u>Kageneckia oblonga</u>	18.86	40.0	7.17
<u>Cryptocarya alba</u>	17.65	34.7	7.52
<u>Colliguaya odorifera</u>	18.95	37.5	7.99
<u>Satureja gilliesii</u>	18.02	31.2	8.89
<u>Quillaja saponaria</u>	18.33	37.6	7.34
<u>Trevoa trinervis</u>	18.15	33.5	8.38
Mean	18.37	36.1	7.82

TABLE 7.--Chemical characteristics related to flammability of foliage of dominant California chaparral and Chilean matorral shrubs. Inorganic nutrient and ether extractive data are for June 1976 in California and November 1975 and 1976 in Chile (Rundel, unpublished data). Energy contents are from Mooney and others (1977).

	Leaf ether extractives	Total ether extractives	Leaf energy content	Leaf phosphorus content	Leaf Ash content
	(% dry wt.)	(% dry wt.)	(kJ g ⁻¹)	(% dry wt.)	(% dry wt.)
California					
<u>Adenostoma fasciculatum</u>	7.76	4.78	21.86	0.17	1.58
<u>Arctostaphylos glauca</u>	7.70	2.53	20.65	.19	2.17
<u>Ceanothus greggii</u>	5.86	2.79	20.93	.22	3.95
<u>Rhus ovata</u>	3.68	2.51	19.35	.23	1.55
<u>Heteromeles arbutifolia</u>			21.20		
<u>Quercus dumosa</u>			20.33		
<u>Ceanothus leucodermis</u>			20.16		
<u>Quercus agrifolia</u>	—	—	19.23	—	—
Mean	6.25	3.15	20.45	0.20	2.31
Chile					
<u>Quillaja saponaria</u>	1.02	0.38	19.38	0.19	2.87
<u>Trevoa trinervis</u>	.22	.41	18.42	.20	4.56
<u>Colliguaya odorifera</u>	1.96	1.91	18.47	.12	1.96
<u>Satureja gilliesii</u>	2.02	.59	18.49	.26	2.97
<u>Cryptocarya alba</u>	2.38	1.45	21.08	.16	2.49
<u>Kageneckia oblonga</u>	3.70	2.67	19.98	.26	3.45
<u>Lithraea caustica</u>	1.80	.80	19.98	.10	1.75
Mean	1.87	1.17	19.49	0.18	3.19

CONCLUSIONS

Although large areas of the world are characterized by frequent natural fires and dominant plant species in these ecosystems exhibit a variety of fire adaptations, we have a very imperfect knowledge of how fire has influenced the structure and productivity of these vegetation types. In fire-adapted ecosystems which are seral in nature, frequent fires allow the maintenance of these early successional species. Many grasslands and pine forests fit this model. In nutrient-limited ecosystems fire may provide an important pathway for rapid decomposition and cycling of nutrients. It is possible that natural selection has operated under such conditions to evolve shrub structures and foliage chemistries which favor high flammability and thus maintenance of early successional stages and/or more effective use of fire-induced patterns of cycling.

While ignition events from lightning are purely physical in origin, the frequency with which potential ignition events produce fires may be profoundly influenced by the structure and chemical composition of the fuels involved. Volatile compounds which ignite at low temperatures may be particularly important in this respect. Once ignition has occurred, the intensity of a fire is strongly influenced by the structure of the fuels in allowing heat transfer and by the energy content of the fuel.

The evolution of canopy form and architecture has traditionally been viewed in terms of photosynthetic adaptation (distribution of leaf area) or water relations adaptation (stem flow). Ecological interpretations of the secondary chemistry of foliage have stressed herbivory or allelopathy. However, if fire-adapted plant species can evolve reproductive adaptation to fire (resprouting from root-crowns, serotinous cones, fire stimulated seed germination) and anatomical adaptations to survive fire (thick bark, epicormic sprouting), it should not be surprising to suggest that they may also evolve structural and chemical adaptations to biologically influence natural fire frequencies.

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FIRE ADAPTIVE TRAITS OF VASCULAR PLANTS

A. Malcolm Gill

Senior Research Scientist
CSIRO Division of Plant Industry
Canberra City, Australia

ABSTRACT

Plant survival, fire-stimulated seed dispersal, fire-enhanced flowering and fire-promoted germination were the four traits examined in relation to various combinations of fire intensity, fire frequency, and season of fire occurrence (the fire regime). While fire selection can be important to the expression of some traits, selective agents other than fires may have an important, even dominant, role.

KEYWORDS: fire, adaptation, vascular plants, survival, reproduction

INTRODUCTION

In one sense "traits adaptive to fire" are all those traits contributing to the successful completion of the life cycle of a species in a fire-prone environment. However, some traits have been given special attention because of the obvious survival or reproductive value they exhibit when subject to fire. These traits are those which conform clearly to Dobzhansky's (1956) definition of an adaptive trait--one which "facilitates survival and/or reproduction of its carrier....".

In the literature of fire ecology, four traits of plants have been given special emphasis. These may be described as those traits which enhance survival during fire--such as protected buds--and those which enhance reproduction--such as fire-stimulated flowering, seed storage on the plant and fire-stimulated dispersal, and real storage in the soil and fire-stimulated germination. These four topics are discussed below.

BUD PROTECTION AND PLANT SURVIVAL

Vegetative survival following severe fires is often remarkable. Trees may resprout from buds protected during the fire by bark if the crown has been scorched, while in fires of lower intensity, where no leaf scorch occurred, the tree may survive and appear unaffected. Shrubs may be razed by fire but buds protected by soil may grow out to restore the canopy. Some rhizomatous herbs may have their leaves destroyed but growth of leaves may continue from protected basal meristems and thus restore their

photosynthetic area; in addition, buried buds may develop shoots. Another variation about this theme of bud protection is provided by many arborescent cycads, monocotyledons or ferns which have buds protected by dense foliage or tightly packed, persistent leaf bases. Below, these topics are examined in more detail.

Bark Thickness and Bud Protection

Excellent examples of the role of bark thickness in bud protection may be found in drier forest of the genus Eucalyptus in Australia. Trees may survive and refoliate even after fires severe enough to consume their canopies. While smaller twigs and branches may be killed in such cases, buds may survive beneath the thicker bark of the larger branches and the bole. When the correlative inhibition of buds by the leaves is removed in this way, they grow out to restore the crown.

Crown recovery in Eucalyptus can be very rapid in some cases. Gill (1978) has recently shown that 5 to 7 m tall crown-fired trees of E. dives had reestablished pre-fire leaf areas within a year and had resumed their normal branching pattern within 3 years. Observation suggested that larger trees in the same area took longer to recover. Variation is expected with tree size and species, but the example is indicative of the rapid responses that are possible from protected buds.

Bud protection beneath bark has been examined implicitly by many authors as they sought to describe the insulating qualities of bark. All researchers have agreed that bark thickness is a particularly important variable (Stickel 1941, Martin 1963, Hare 1965, Kayll 1966, Reifsnyder and others 1967, Gill and Ashton 1968, McArthur 1968, Vines 1968). Those who have attempted to measure thermal diffusivity, a variable which expresses the rate of penetration of a temperature wave, have emphasized the importance of bark thickness in temperature penetration of barks. For example, Reifsnyder and others (1967) declared that "bark thickness appears to be the primary factor determining whether a tree is fire resistant or not," while Martin (1963) in discussing his results for three pine species and seven hardwood species noted that "thermal diffusivity is nearly constant over wide ranges of density, moisture content and temperature." Despite these results, some research using direct application of high-temperature sources to tree trunks (or sections) has suggested that bark characteristics of different species were significantly different in relation to temperature penetration (Stickel 1941, Hare 1965, Gill and Ashton 1968). These differences may reflect the importance of bark flammability (Vines 1968), a characteristic not yet given serious consideration.

Surprisingly few studies of bark-thickness variation have been made within a fire context considering its importance to vegetative survival. It is known, however, that species, girth, sample height, and site history all affect this variable (Gill and Ashton 1968, Nicholls and Phillips 1970, Smith and Kozak 1967). Among Eucalyptus spp. of 100 cm girth at 1.5 m height for example, bark thickness may vary from about 9 mm (E. papuana) to about 34 mm (E. obliqua). Increased girth is usually reflected in increased bark thickness, and both these trends may be expected with age. Site effects may be associated with fire history through the mechanisms described below.

The thick but loosely fibrous barks of some eucalypts are particularly combustible and fire occurrence may thereby decrease bark thickness. Another mechanism of bark loss occurs in the smooth and moist bark of many other Eucalyptus spp., however. Abscission in these cases is induced; heat-killed bark is shed following the formation of an abscission layer beneath the dead bark. If the thickness killed is less than the total thickness, the tree survives from living buds.

With the loss of bark through combustion or induced abscission, protection of stem buds is reduced. To offset this, the tree begins to restore bark thicknesses. At the same time, the plant community in which the species occurs is producing fuel for future fires. Whether or not the tree returns its bark thickness to prefire

levels before the next fire depends on the rate of fuel accumulation and the chances of ignition. Upon fire occurrence, fire intensity affects the amount of bark lost. Thus, fire frequency and fire intensity are important factors affecting the amount of protection an aerial stem may provide its buds.

The features described here--particularly temperature penetration of bark and bark losses in fire--have been described as though the effects were uniform over the whole tree. This is not necessarily true. Many examples of asymmetric death about the tree bole can be given because the fire scars formed as a result of unequal effects of fire over the tree are often prized for the dating of past fires (Arno and Sneek 1977).

Fire-scar formation in trees reflects an important aspect of survival of trees in fires. If all heat is evenly distributed about the bole of a tree, it is possible to envisage a point where just sufficient heat is provided for death to occur. On the other hand, if the same amount of heat is differentially redistributed around the bole according to bole size, windspeed, and possibly fire intensity, as Gill (1974) has indicated, the tree may survive (Tunstall and others 1976).

Subterranean Protection of Buds

Soil is an effective insulator (Al Nakshābandi and Kohnke 1965) and heat inputs from fires are small in relation to the total heat released. Packham (1970) found convective heat from a surface fire to be about three times that of radiated heat. As most convective heat rose, and only a portion of the radiated heat entered the soil, only about 5 percent of the heat from the fire heated the soil (Packham 1970). For these reasons, the subterranean position of buds is a well-protected one in surface fires. In peat fires, where the substrate itself is destroyed, the depth of burning becomes very important (as implied by Flinn and Wein 1977).

Rhizomes often support subterranean buds in ferns, monocotyledons, and dicotyledons. Root buds seem to be a common feature of some dicotyledons while buds at the bases of vertical stems are found among dicotyledonous shrubs. In some cases the buds at the bases of stems may multiply to form a local woody swelling known as a "lignotuber" (Kerr 1925).

To examine the nature of selective forces on basal buds, the example of the lignotuber is considered here according to its occurrence among species of the genus Eucalyptus. There are about 400 woody species in this Australia-wide genus (Pryor and Johnson 1971) and most of them have lignotubers. The trait is absent from species in the best sites (where growth rates are rapid and mature tree heights tall) and most obvious in the sites of poorest quality (multi-stemmed, slow-growing shrubs or small trees). To generalize, the most stressful sites (poor soils, low light intensity, low rainfall, low temperature) have the greatest frequency and prominence of lignotuberous plants. Thus, the lignotuber in Australian Eucalyptus may perhaps be regarded as an adaptive trait for recovery and persistence under stresses of many types including fire occurrence (Gill 1975).

Organs similar to lignotubers have been reported from Africa (White 1977). There, they are confined to the tropical and subtropical savanna regions, and are diverse taxonomically. White (1977) examined a number of hypotheses for their evolution in his "preliminary review" and concluded that they evolved "not primarily in response to fire, nor to frost as had previously been supposed, but as a response to the unfavorable edaphic conditions."

In Brazil, analogues of the lignotuber have been called "xylopodia" (Eiten 1972). They occur on plants with short-lived shoots and appear similar to those in Africa

as described by White (1977). Eiten (1972) associated this form with survival from fires. Australian examples would appear to have longer-lived shoots generally, although the rhizomatous eucalypts described by Lacey (1974) have short-lived shoots because of annual fires.

For many shrubs, basal sprouting may be common after fire has destroyed the foliage, but these sprouts may arise from a region in which no basal swelling is obvious. This is particularly so for those species which respond from root suckers or rhizomes, of course.

Survival of buds during fire depends also on what Naveh (1974) calls the "vitality" of the plant. Taking a broad view of "vitality" as those plant factors affecting resprouting after fire, we might distinguish the age of the plant, as well as its physiological fitness to withstand fire, as an important variable.

In the seedling stage, the young shrub may be particularly vulnerable to fire unless it has particular adaptive traits--such as those described as "cryptogeal germination" by Jackson (1974) in Africa. In old stands vitality may gradually decrease. Kayll and Gimingham (1965) found that fewer of the older stems of Calluna in heathlands regenerated from clipping and burning, while Miller and Miles (1970), on the other hand, found that the proportion of shoots regenerating from stands of different ages was similar. If forest cutting is any indication, a decline in response with age or size may be expected at some stage; P. S. Johnson (1975), for example, found a decrease in the percentage of stumps sprouting as stem size increased.

Vitality can also change during the year and responses to cutting illustrate this well. Cremer (1973) found that for evergreen hardwoods in Tasmania, seasonal effects were evident in 1- to 3-year-old seedlings, but for 15- to 30-year-old plants response was poor and no trend was evident. In Californian chaparral, Jones and Laude (1960) studied Adenostoma and found that there was a seasonal variation in survival whether or not the plants were cut, burned, or treated with herbicide.

Survival is also influenced by fire severity (Naveh 1974) but there is little information on this. There are data, however, for the effects of repeated fires. Grano (1970), for example, found that numbers of understory hardwoods in pine forests of the southeastern United States were reduced by high fire frequencies. Eleven annual burns killed 85 percent rootstocks while biennial burns eliminated sprouting on 59 percent.

The examples given above are largely those for woody plants. Similar principles may be expected to apply to nonwoody plants but such examples seem to have received less attention. Emphasis has been given to effects of fire severity, fire frequency, and season of burn as important aspects of selection by fire.

Bud Protection by Leaf Bases

Some plants survive fire by the protection afforded their buds by tufted crowns. These may be at ground level or on aerial stems. In the former case many are tussock grasses while the latter are genera like Pandanus. As a group, these plants with tufted crowns are very fire resistant. As case studies, the monocotyledons are appropriate but are only examples of habits that are more widespread taxonomically, viz, in tree ferns and cycads.

Holttum (1955) has given an excellent description of the tufted or tussock condition and its development. Because of the lack of a cambium, plant expansion depends on the production of roots which arise from nodes of the stem. With short internodes there are many sites for the production of new roots and, with a sympodial growth habit, these may be produced at ground level. In this way, short internodes and sympodial growth lead to the production of the tufted habit.

Examples of the tufted habit among grasses are numerous. The pampas grass of Argentina (Cortadaria selliewana), often cultivated for horticultural purposes, is an excellent example. Other examples may be found in grasses from the tropics (Smith 1960) to alpine temperate regions (Mark 1965a).

The tufted crown may be found on aerial stems. In these cases the tuft of leaves is usually found to terminate one or a few branches rather than the many hundreds which may form the ground-level tussock. The apical buds of the branches are protected by the rigid leaf bases of the apical leaves. Excellent examples are provided by Pandanus in Hawaii (Vogl 1969) and elsewhere, by Palmae throughout the tropics, and by Xanthorrhoea in Australia (Gill and Ingwersen 1976).

In some cases the closely packed leaf bases persist long after the major photosynthetic part of the leaf is lost. Suffrutescent and arborescent Xanthorrhoea spp. are good examples. These provide deep and effective insulating materials for stems while the moist, densely packed crowns are ideally suited to protecting apical buds. Fire resistance also follows from the dispersed nature of the stem vasculature of monocotyledons described by Zimmermann and Tomlinson (1972).

Following burning of the crowns of tufted monocotyledons, regrowth of leaves takes place by intercalary growth. Unlike dicotyledons which develop new leaves, the old leaves of monocotyledons continue to grow from protected bases. Because of this, monocotyledons are often the first plants to provide new green material after fire. Examples are the Xanthorrhoea described by Specht and others (1958) and the many tussock grasses of the world.

The tufted habit of monocotyledons is widespread. Arborescent examples are more common in the tropics (and not always exposed to fires) while nonarborescent forms are developed extensively in temperate areas. The form provides excellent fire resistance and occurs over an enormous range of environments with a similar variation in fire regimes. Holttum (1955) stressed the importance of the lack of a cambium in the derivation of the growth habits described, rather than adaptation to a seasonal rest as had been described earlier by Sargent (1903, from Holttum 1955). It might be noted in passing, however, that many monocotyledons that do have a cambium--such as Xanthorrhoea australis and others (Tomlinson and Zimmermann 1969)--have many similar characteristics to those tufted monocotyledons without a cambium.

Bud Protection and Resprouting After Fire

Diverse mechanisms account for survival during fires. The traits responsible are found among diverse taxonomic groups. Bark thickness is an important trait in bud protection in arborescent conifers and dicotyledons; the tufted crown form offers bud protection to apical buds among tree ferns, cycads, and monocotyledons; while, the subterranean position of regenerative buds is common to many species of ferns, cycads, and angiosperms. As a group, the conifers tend to be more susceptible to single fires than others.

Within species and populations, the traits responsible for survival (or otherwise) during a fire may vary considerably. Bark thickness varies between populations of Pinus banksiana and has been thought to be under strong genetic control (Schoenike 1976). Similarly, lignotuber expression can vary widely within a species (Karschon 1967) and is under genetic control (Pryor 1957). Tussock density varies ecotypically in the grass Themeda australis (R. H. Groves, personal communication).

Each protective mechanism varies developmentally so susceptibility of a plant to a fire may vary during its life cycle. Bark may be very thin while the tree is small, be particularly thick at maturity, and decline in senescence. Apices of some species

may occur at the surface of the soil at germination but become buried by a variety of mechanisms during development (e.g., Tomlinson and Esler 1974 for some monocotyledons). Grass tussocks often begin small, grow to maturity, and senesce later; fire sensitivity may vary through these stages.

One or other of the protective mechanisms described occurs throughout the fire-prone regions of the world--and in some non-fire-prone regions as well. Where the fires do occur, they may be of rare or frequent occurrence, may be of high or low intensity, and occur at various times of the year. Fire may select some forms according to its intensity, frequency, and seasonal occurrence but it must be stressed that the traits described are subject to many selective pressures in the diverse environments in which they occur. Fire--in all its combinations of properties--is only one of these agencies!

FIRE-STIMULATED FLOWERING

Among fire-resistant plants, the curious phenomenon of fire-stimulated flowering has been widely observed but little studied. By far the most common observations of this habit have been in species of monocotyledons although rare cases among dicotyledons have been reported (Gardner 1957, Rogers 1975). Examples come from the Gramineae, Orchidaceae, Iridaceae, Liliaceae, Amaryllidaceae, and Xanthorrhoeaceae. Some of these are described below.

In the tussock grasslands of montane New Zealand a dominant species, Chionochloa rigida, has a fire-stimulated flowering. Rowley (1970) recorded this fire response in terms of the numbers of tussocks flowering and the numbers of inflorescences produced per flowering tussock. She found that all those tussocks which were burned in spring flowered and produced an average of 46 inflorescences. Contrasted with this was the behavior of unburned tussocks which had only a 12 percent flowering and a meager 1.2 inflorescences per flowering tussock on average. Clipping of tussocks produced an intermediate response; 24 percent of tussocks flowered with an average of 13 inflorescences per flowering tussock. While these results are clear, they represent only a portion of the fire-flowering picture because the flowering response depended on the actual year in which experimentation took place.

In unburned stands of Chionochloa, profuse flowering occurred in some years but not in others (Mark 1965a). This phenomenon had a marked effect on the response to burning. If burning took place in the spring of a nonflowering year (for unburned tussocks), a strong flowering response was elicited in treated plants as described above. If, on the other hand, burning took place in the spring of a flowering year (for unburned tussocks), a flowering inhibition occurred (Mark 1965a).

When a flowering response occurred it was evident in inflorescences the second flowering season after spring fires. Floral induction took place during the long days of summer when temperatures were relatively high and fluctuations in temperatures were marked (Rowley 1970). Thus, tussocks which were burned in spring were exposed to these inductive conditions in summer and flowered a year later, while tussocks burned in autumn had a flowering response nearly 2 years after treatment (Mark 1965a).

The profuse flowering observed in unburned tussocks in certain years was associated with unusually warm summers (Mark 1965b). Burning prior to induction was thought to alter the microenvironment of the tussock and thereby raise tussock temperature, or its fluctuations, to inductive levels (Rowley 1970). Burning following an inductive summer presumably destroyed young inflorescences; whether or not there was a compensatory increase a year later was not reported.

Increased flowering in grasses due to fire has been reported particularly in North America (Daubenmire 1968, Wein and Bliss 1973). Inquiries for examples in Australian

grasslands, by contrast, have been fruitless. In the prairies of North America, Old (1969) has produced a comprehensive report on fire and flowering which enables a comparison between the New Zealand and North American examples. Mark (1965a) considered that for the New Zealand grassland "the analogy with the prairie grasses is not very close."

Old (1969) found that burning of the Illinois prairie caused a tenfold increase in flowering, a stimulation less than that reported by Rowley (1970) in New Zealand. In the U.S.A., mulch reduced flowering but in New Zealand it had no effect. This result may be associated with a shading effect because shade depressed flowering in Old's (1969) study but not in that of Mark (1965b). In both examples, ash had no effect but applications of nitrogen (applied in U.S.A. only) had a marked effect. In New Zealand, Connor and Powell (1963) added sulfur and phosphorus but there was no flowering response. In both Illinois (Old 1969) and New Zealand (Rowley 1970) the microclimatic conditions following burning had an important influence on the response. Thus, while similarities exist in the two examples, there are significant differences in mechanism of the response.

Among terrestrial orchids there are many examples of fire-stimulated flowering (Naveh 1974, for Israel; Hall 1959, for South Africa; and Gill 1980, for an Australian summary). While the response has been widely noted, it has been little studied. However, Erickson (1965) noted that applications of wood ash stimulated some Western Australian orchids to flower, and Naveh (1974) suggested that increased light intensity after fire may have been the flowering stimulus.

In South Africa, the flowering of the geophytic Amaryllidaceae, Iridaceae, and Liliaceae following fire is a notable feature (Kruger 1977). Martin (1966) catalogued the timing of the response to fire for a number of species but was unable to reach any firm conclusion as to the nature of the stimulating agent. He rejected ash as a factor but suggested that possible factors of importance could be removal of competition, increased soil temperatures, and greater diurnal temperature fluctuations.

Xanthorrhoea spp. in Australia provide some interesting examples of postfire flowering. A marked stimulation of flowering by burning was shown by X. australis in secondary grassland (Gill and Ingwersen 1976). Clipping the crowns of these suffrutescent plants also stimulated flowering as did injection of an ethylene-releasing chemical. From these experiments Gill and Ingwersen (1976) considered that the flowering response was triggered in treated plants by enhanced ethylene levels, in a similar way to the response of ethephon-sprayed pineapples (Bondad 1976).

The timing of inflorescence emergence in X. australis was changed by burning (Gill and Ingwersen 1976), a phenomenon common to a number of other examples. Mitchell (1922), for example, found that flowering induced by fire in Asparagus sp. was much earlier than normal (Kruger 1977). This suggests that the timing of burning of plants may influence the timing of inflorescence emergence. Such has been the case for the grass Chionochloa (Mark 1965a) as described earlier, and for the South African geophyte Watsonia described by Kruger (1977).

In most examples of fire-stimulated flowering, there are individual unburned plants which also flower; this was certainly the case in X. australis (Gill and Ingwersen 1976). Such observation suggests that there is a certain amount of genotypic or phenotypic variation in the response. Interspecific differences have been noted by F. Ingwersen (personal communication) for Xanthorrhoea spp. burned by the same fire in coastal New South Wales. Circumstantial evidence for genetic variability in the flowering response after fire comes from the alternative behaviors of Sorghastrum nutans (Daubenmire 1968) although the experience of alternative behaviors according to year of treatment in Chionochloa elicits caution in the interpretation of these results.

Many mechanisms appear to operate in the triggering of flowering by fire. The results are similar, however, in that prolific flowering follows. While the ecological significance of such flowering has been little studied it is likely to be found in enhanced seedling establishment. The latter may be a consequence of greater seed set, low on-plant predation of seeds, or lower predation of seeds following dispersal.

In the New Zealand example of postfire flowering, Mark (1965a) found that seed set was greater in the prolifically flowering burned plants than among the sparsely flowering unburned grass tussocks. Seed set in untreated plants in years of prolific flowering was very variable (Mark 1965b). Prolific but irregular flowering was thought to have selective advantage, however, in that the seed supply which resulted was an unreliable one for predators such as the larvae of gall midges (Mark 1968), viz, native Diptera of the Cecidomyiidae (Mark 1965b).

In a similar fashion, A. M. Gill (unpublished) has suggested that prolific flowering at irregular intervals might be an important factor in the success of seed set in Xanthorrhoea australis. Larvae of the moth Hyaletis latro predated inflorescences and often caused severe losses in seed production. It was hypothesized that predator satiation occurred in years of abundant flowering because these followed years when populations had been reduced to low levels by a scarcity of substrate.

The two examples above of the selective advantage of irregular prolific flowering as stimulated by fire have emphasized the role of predispersal predation by insects. It would be unwise to assume that this is always the case. Fungal pathogens, postdispersal predation, more effective pollination, and improved seedbed conditions may also be involved but their impact and importance will not be known until further examples have been studied.

SEED STORAGE ON THE PLANT AND FIRE-STIMULATED DEHISCENCE

For many shrubby or arborescent species, seed storage on the plant is an important aspect of the life cycle. This is particularly so where fire-sensitive plants are involved because this stored seed becomes the means of persistence of the species. Below, the ecology of one such species, Eucalyptus regnans, is outlined and then followed by some details of its seed development and seed fate. With this information, a number of hypotheses are formed regarding the seed-storage habit.

Eucalyptus regnans of Australia

This species is the famous tall hardwood tree of southeastern Australia. It is a rapidly growing tree (Galbraith 1937) which usually occurs in one-aged stands (Ashton 1958). Regeneration has taken place following killing bushfires (Galbraith 1937) providing that mature plants were present. Fires have been relatively rare in the past (say 200 to 300 years apart) but have been known to occur at intervals less than about 15 to 20 years, a frequency which can cause local extinction of the species. The first fruiting of any consequence in the field seems to take place at about this time although seed production can be quite prolific in some individual trees at 20 years of age (Eldridge 1964).

After killing fires, regeneration of the species depends on the seed stored in the canopy at the time of fire. With such a dependency it is appropriate to examine the development of the fruit, the storage of seed, seed dissemination, and the fate of seed.

Development of the capsule of E. regnans has been described by Ashton (1975) and Cunningham (1960) as follows: Inflorescence buds form axillary to currently expanding leaves. These buds have an involucrel operculum which abscises to expose 20 to 40 minute flower buds about 1 year after initiation (i.e., at time $t = 1$ year). Flowering

place approximately 2 years after initiation. Mature but green capsules have formed by $t = 3$ and most seed shed occurs between $t = 4$ and $t = 5$ when the water supply to supporting branches is lost and capsules dry out. Seed storage is short, being effective for about 2 years.

Ashton (1975) has highlighted the selection process as it occurs during development. Large losses in numbers of buds and fruits may occur due to "competition" or to various biological agents. Ashton (1975) noted the losses of inflorescence buds due to gall insects. Umbellate buds may be lost to fungal infection and to the gall-wasp Megastigmus as well as to abscission: Up to 40 percent buds may absciss while up to 25 percent may be galled. From 2 to 3 years after initiation, up to 90 percent of flower buds present at the start of this time period may be lost to fungal and insect attack. Beyond this stage, capsule losses may be negligible for the next year. If fruits remain alive for many years they may become embedded in the host branch or become colonized by lichens; in these ways they may become nonfunctional.

While the general pattern of losses of buds and capsules has been outlined for the period of development of the seeds, no information has been given above concerning the year-by-year variability in the size of the crop. In this case, such a consideration is most important.

Year-to-year variation in crop size is imposed on a general trend in production according to stand age. Thus Ashton's (1975) figures for stands of about 200, 50, and 25 years of age suggested that average flowering abundances were in the ratios 4.5 to 1.8 to 1 for the three stands respectively. These average figures, however, conceal the enormous periodicity in production.

Flowering periodicity in the species may be considered biennial as a heavy crop follows a light one. The ratio of flower-bud numbers from one year to the next may be as high as about 40:1 (Ashton 1975). In figure 1 the maximum ranges in flower abundance for the years 1953-57 are superimposed on the general trend associated with stand age. Note that the biennial bearing range of the mature stand exceeds that for the trend values for the stands from 25 years to 200 years of age.

The biennial flowering of this eucalypt is often, but not always, reflected in the size of the fruit crop. The seed crop following an abundant flowering could be quite low if fertilization fails, for example (Aston 1975). In general, however, one might expect parallel behavior between flower and fruit yields.

While the biennial-bearing habit is probably a consequence of developmental patterns of flowers on the shoots, it is tempting to suggest that its ecological significance is to be found in the population trends of the insect predators of reproductive organs. These organisms may be disadvantaged by alternate periods of shortage and abundance while reproduction of the tree may be enhanced by large crops which satiate the predator. Support for this idea comes from the generally higher ratios of buds to flowers in years of high bud production compared with those for years of poor bud production; percentage of flowering buds from the total bud crop for a good year in comparison to a poor one was usually in the ratio of 2 or 3 to 1 (Aston 1975).

Long-term visual data for the flowering of E. regnans have also been reported by Ashton (1975). A major feature of these data was the very low flowering abundance in the years 1968-70 during an unusually severe drought. "This succession of flowering failures very greatly depleted the storage of fruits in the canopy and would have placed the regenerative capacity of this forest in jeopardy had serious top fires occurred" (Ashton 1975).

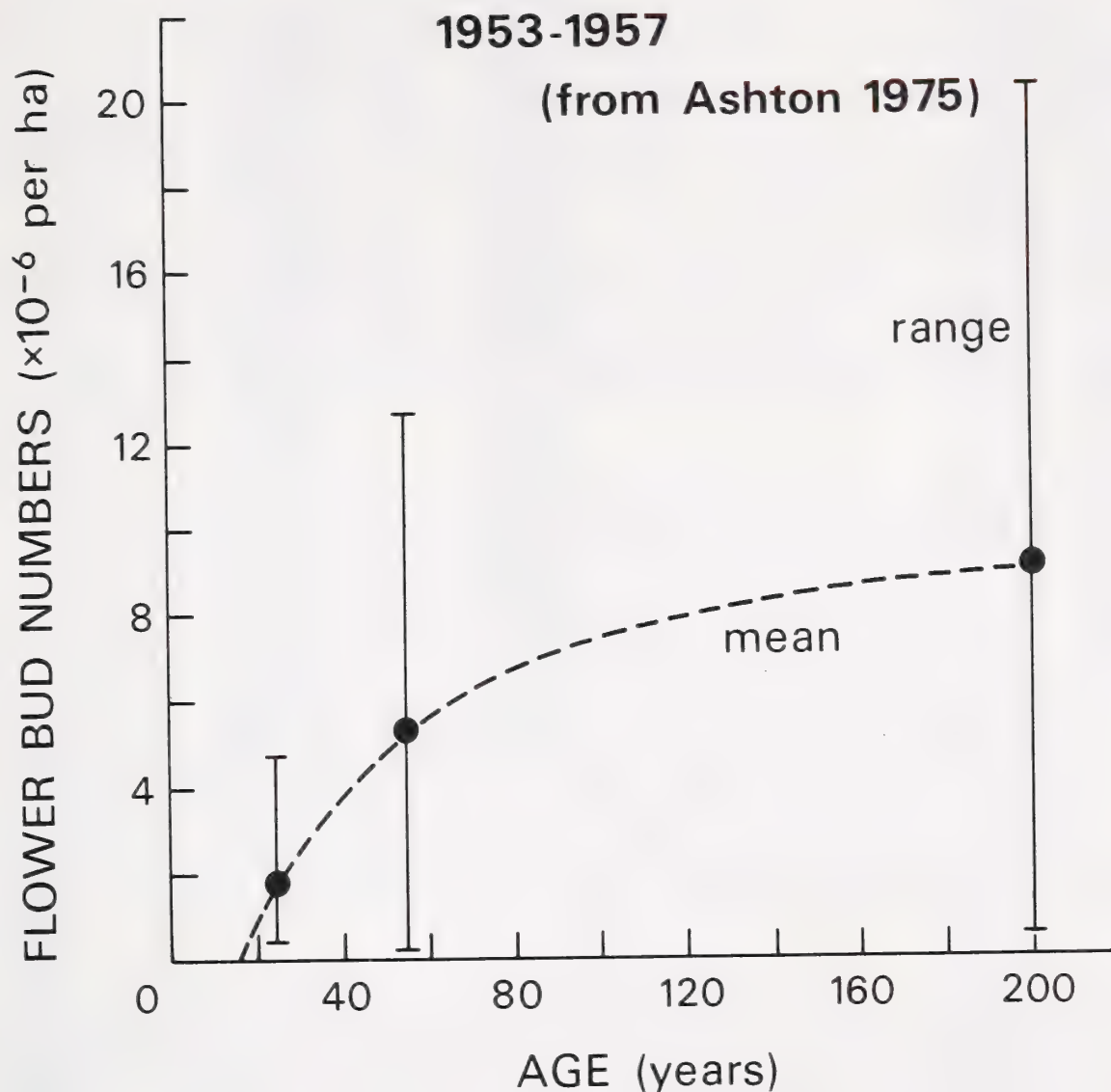


Figure 1.--Eucalyptus regnans: ranges and averages for numbers of flower buds (millions per hectare) for the years 1953-57 according to stand age (Ashton 1975 data).

Consideration of the development and behavior of flowers and capsules on the tree has led to three hypotheses concerning the seed-storage habit in this species, all of which are based on the assumption that the species must maintain an adequate seed storage on the tree at all times if it is to regenerate following fires. These hypotheses are: seed storage is necessary to dampen fluctuations in seed supply caused by biennial flowering; seed storage is necessary to maintain a seed supply when fertilization has been poor; and seed storage is necessary to maintain seed supplies over periods of drought when flowering is poor.

The subject of the significance of seed storage in this species cannot be left here. It is important to follow the cycle of reproduction through to the stage of seedling production to provide further data and other hypotheses. To examine losses between canopy-stored seed and germination, with and without fire, data are presented graphically (fig. 2) and outlined below.

Seed formed from a good flowering year appears to be released subsequently over a 2-year period (Cunningham 1960). In this way, fluctuations in seed shed should be much less marked than those for flower numbers. Without fire, then, half the seed crop is assumed to be lost annually. About 75 percent of this seed falls as free seed,

Eucalyptus regnans

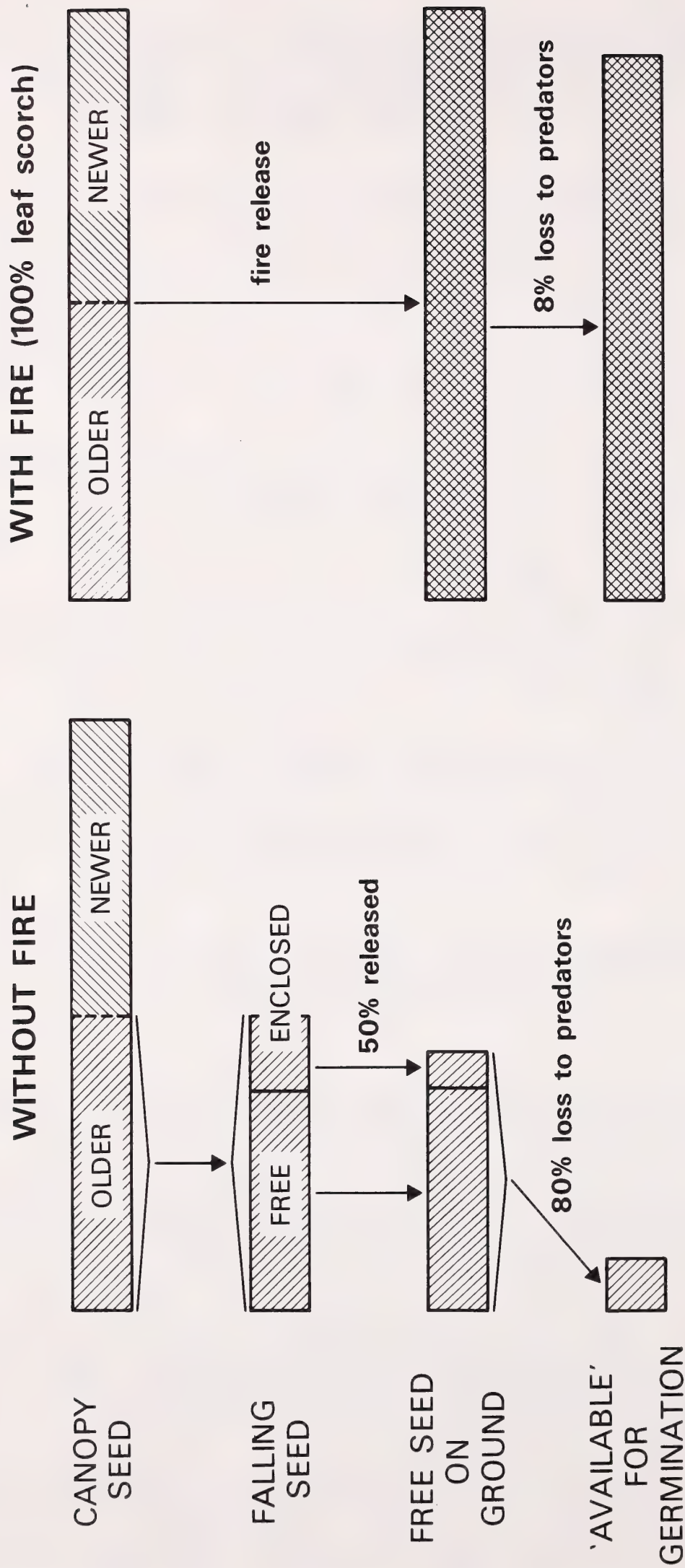


Figure 2.--Tentative interpretation of data for seed fate in *Eucalyptus regnans* (with and without a crown-scorching fire) using data from Ashton (1975), Christensen (1971), and Cunningham (1960).

the remainder in capsules (Cunningham 1960). Some free seed may be spilled from capsules eaten by cockatoos and parrots. These birds spill about 30 percent viable seed (Ashton 1975). For capsules falling intact about 50 percent may subsequently open and release seed (Cunningham 1960). Seed on the ground is severely predated by ants and other insects (Cunningham 1960 estimated 80 percent loss), a loss presumably spread over the 4-month period of seed dispersal (Cunningham 1960).

It is highly probable that all seed on the canopy would be released if the crown is completely scorched by fire, viz, half the previous year's crop plus the current year's crop. If these assumptions are correct the storage on the plant will vary according to the abundance of the previous year's crop (and parallel flowering behavior), but this has been ignored in figure 2 which shows equal storage of seed from 2 years' flowerings.

An important point is that the seed released from the canopy upon complete scorch will fall in a few days--by analogy with behavior of E. diversicolor in Western Australia (Christensen 1971). No study of insect losses under these circumstances has been made, but if we assume that the same rate of loss occurs as that derived from Cunningham's (1960) data, viz, 80 percent loss from 41 units of seed over 4 months (2.05 units per week), and apply it to the fire situation where 200 units of seed fall in 4 weeks, only 8.2 units are lost. Clearly, these data are incomplete and unsubstantiated but they begin to provide a picture of various factors influencing selection for seed storage. The data suggest that seed supply for germination after fire will be very much greater than that under normal seed fall in the interfire period. Thus a fourth hypothesis is suggested; that seed storage on the canopy and fire-stimulated release causes predator satiation and enables greater seed numbers to be available for germination.

Seedlings in the unburned forest soon die due to lack of light, fungal attack, and browsing (Ashton 1956, Ashton and Macauley 1972). In the nutritionally enriched, well-lit seedbed that follows fire, however, seedling survival is greatly enhanced. Thus, fire-stimulated dehiscence of canopy-stored seed allows seedling development on a physically and chemically improved seedbed, our fifth hypothesis.

Many other eucalypt species have a similar seed storage on the canopy and have fire-stimulated dispersal but have vegetative means of survival. They lack dependence on seed for regeneration. As a corollary to the E. regnans example it is suggested that in these species flowering may be less reliable due to poorer environmental conditions, while seed predation remains just as intense. Failure to maintain reliable crops and an unpredictable and often unreliable seedbed after fire may have led to selection for vegetative resistance in these species.

Closed-Cone Pinus and Other Examples

The seed storage phenomenon of some Pinus spp. is a very variable one. When storage does occur, however, it may be for a very long time, unlike Eucalyptus.

Pinus contorta is a good example of a species with a serotinous or closed-cone habit. Young trees appear always to have open cones whereas older trees may have closed or open cones (Lotan 1975). Within a stand, serotiny can also vary widely as Lotan (1975) has shown for samples in the Rocky Mountains. Between-stand variation also occurs but gradients of universal relevance are hard to find. Thus Lotan (1975) found a correlation between degree of serotiny and elevation in some cases but not in others.

Unlike Eucalyptus regnans, seed crops in serotinous lodgepole pine stands appear to be uniform in time. Indeed, Smith (1970) noted that the "frequency of fires, which is definitely a property of the physical environment, selects for serotiny and the

constancy of cone crop size in lodgepole pines" (my emphasis). On the other hand, it appears that nonserotinous crops are less constant because cone crop failure in such populations has been reported (Mowat 1960). Smith (1970) suggested that squirrels caused selection for harder cones in constant seed crops but selected for even greater fluctuations where these already occurred. Whether or not fluctuations and lack of serotiny could be associated in lodgepole pine was not clear. Thus while squirrels are important predators of seed and may select cones of individual trees in preference to others (Elliott 1974), their actions do not appear to affect serotiny directly. Rather, fire properties appear to be selective for both serotiny and bark characteristics.

For both P. contorta (Lotan 1976) and the closely related P. banksiana (Schoenike 1976) there appeared to be a correlation between bark thickness and the degree of cone serotiny. Where bark was thickest, serotiny was least; where bark was thinnest, serotiny was greatest. Furthermore, where serotiny was least, fires appeared to occur with lower intensity (Lotan 1976) whereas in areas where serotiny was greatest, fires apparently had been of higher intensity. Perhaps low-intensity fires, tree survival, and open cones were associated on the one hand, and high-intensity fires, tree death, and closed cones were associated on the other.

To understand these examples--and others like them--it would be pertinent to study a series of stand variables at each location (not serotiny alone) along the lines of Schoenike's (1976) study. It seems possible that trees with open cones may occur largely in relatively poor sites where fuels are only slowly accumulated and trees are well spaced; mineral soil remains exposed for many years and seedling establishment from open-cone parents occurs as Lotan suggested (1967). On good sites, rapid fuel accumulations, dense stands, lack of mineral soil, and serotiny may occur together. Few data are available to check these ideas but Schoenike (1976) found a correlation between serotiny and stand basal area, and Rudolf (1958) noted the mineral-soil requirement for regeneration of P. banksiana.

Many genera produce seed which is stored on the plant and released at the time of fire. In Australia, Gardner (1957) mentioned examples from the families Cupressaceae, Casuarinaceae, Proteaceae, and Myrtaceae; many of these typically occur in heathlands. In South Africa, Williams (1972) mentions Proteaceous examples in his taxonomic revision of Leucadendron. Around the Mediterranean Sea, populations of Pinus halepensis and P. brutia occur with serotinous cones (Naveh 1975).

Significance of On-Plant Storage of Seed

In the Eucalyptus regnans example, five hypotheses were generated; three concerned the dampening of fluctuations in seed crops between years; one concerned postdispersal predator satiation; and one concerned the nature of the seedbed. All were concerned with the maintenance of a seed storage to be released at the time of fire for the perpetuation of the species.

The five E. regnans hypotheses do not all apply to the other examples mentioned above. Details of development and selective agencies vary. However, in all cases, selection for a seed supply, available when the seedbed was receptive, occurred. Fire may provide the seedbed and the trigger for seed release. According to the reliability of the climate, or the timing of seed production, a set of fire-susceptible or fire-resistant attributes may accompany the storage habit.

The fire regimes which are associated with this habit are many. The E. regnans fires have an optimal frequency of the order of once in 200 or 300 years and intense fires at these times are advantageous. Many fire-resistant eucalypts would have a shorter interval between fires and variety of fire intensities. Heathlands would vary again from these examples.

There is a general dearth of information about the morphology, physiology, and ecology of seeds stored in soil and released by fires. However, for those seeds known as "hard" seeds, there is an extensive agricultural literature. For seeds in drupes--such as some Epacridaceae, Proteaceae, Rosaceae, and Myoporaceae--little is known of fire effects on germination, while for Californian fire annuals a picture of allelopathic inhibition of germination and its release by fire has been drawn (Muller and others 1968). In this section, emphasis is placed on the "hardseededness" condition because this is the most researched.

"Hardseededness" in the present context includes all those seeds with a physical barrier to germination except those with a woody endocarp. The property is typified by lack of imbibition, swelling, and softening when exposed to water. When the seed coat is scarified, however, germination is prompt under laboratory conditions.

While the hardseeded condition is best known in legumes, it is found in a taxonomically diverse flora. Ballard (1973) lists as examples the families Cannaceae, Convolvulaceae, Geraniaceae, Liliaceae, Leguminosae, and Malvaceae although there are undoubtedly others in members of other families. The list includes woody and herbaceous species, perennials, and annuals. Not all genera, nor all species of these families, necessarily have hard seeds. Rather, the trait is a very variable one at genus, species, and population levels.

During growth on the plant, the seed matures to a stage where germination is possible but no hardseededness occurs. As development continues the seedcoat becomes impermeable but the embryos are still viable--the typical hardseeded condition. These stages have been beautifully illustrated by Sidhu and Cavers (1977) for Medicago lupulina, a legume.

As development proceeds through the stages mentioned above, there is a general decrease in moisture content. When moisture contents are relatively high, impermeability is easily reversed, but at low moisture contents impermeability becomes persistent, and special treatment is required to overcome it (Quinlivan 1971).

In the laboratory, special treatments for removal of dormancy include percussion and scarification (Ballard 1973); exposure to sulfuric acid or boiling water (Jones 1963); or even exposure to radio frequency electric fields (Ballard and others 1976). In the field a number of variables have been held responsible for seed "softening": these include fire (Christensen and Kimber 1975), fluctuating soil temperatures (Quinlivan 1971), and natural scarification (Went 1955).

Hardseededness within a species or population is usually variable. In most cases some soft seed is produced among the hard (Floyd 1966, 1976; Jones 1963; Preece 1971). This variation could be due to developmental stage, field softening, or genetics. That the latter could be important is indicated by the example of Acacia cyclops, a Western Australian sand-dune shrub introduced to South Africa in order to bind sand dunes (Roux 1961). Unfortunately, the species is now a problem weed in South Africa.

There is some nomenclatural variation concerning this species and this engenders caution in the comparison to be made between the South African and Western Australian populations below. In the past, the species in South Africa has been called A. cyclops, A. glaucophylla, and A. cyclopis (Roux 1961) but recent literature (Taylor 1977) favors the first of these. In Western Australia, the species is known as A. cyclops (Christensen and Kimber 1975).

Acacia cyclops is a particular problem to native plant species conservation in the Cape of Good Hope (Taylor 1977). Large seed stores have built up in the soil--to

the extent of 250×10^6 per hectare (Taylor 1977). The species has responded to frequent fires by spreading and has done this at the expense of the indigenous flora (Roux and Middlemiss 1963, Taylor 1977).

The germination of seeds of A. cyclops has been studied by Jones (1963) in South Africa, and Christensen (1978) in Western Australia. Jones (1963) found that 1 percent and 30 percent of untreated seeds had responded after about 1 and 2 months of testing respectively; artificially scarified seeds had 92 percent germination at both 1 and 2 months; exposure to dry heat at 80°C for 30 minutes gave 18 percent germination at 1 month and 68 percent at 2 months. By contrast, Christensen's (1978) data showed no increase in germination due to heating compared with the control seeds: exposure to 90°C for 30 minutes (or 3 hours) gave no change in germination.

The major difference between the habitats of A. cyclops in Africa and Australia seems to be the frequency of burning. Taylor (1977) noted that the South African vegetation in which it occurs was burned frequently. In Western Australia, Christensen and Kimber (1975) noted that the habitat was "rarely subject to fire." Perhaps hard-seededness has been strongly selected for in Africa from an Australian stock with very low hardseededness? The situation warrants further study.

In the above example, fire frequency was the only fire variable mentioned. This has probably an indirect effect only on hardseededness although it must have an influence on the size of the soil seed pool. However, any effect of fire intensity, in this example or elsewhere, would appear to be direct because temperature and its duration have a strong effect on germination and survival. Floyd (1966), for example, produced data which illustrate the interrelationship between length of exposure and temperature; long periods at relatively low temperatures elicited the same germination response as that obtained through exposure for a shorter period at higher temperatures. Furthermore, field data of Christensen and Kimber (1975) suggested that severe fires promoted germination but also destroyed considerable quantities of soil-stored seed.

Too few data are available on the effects of single and repeated fires on the soil-seed pool. This is not to say that no work has been done. Keeley (1977) has carried out detailed work in Californian chaparral; Floyd (1966, 1976) has described studies in logged forests in Australia; and E. A. Johnson (1975) has set the scene for interesting studies in North American forests through his observation that soil populations of seeds decrease polewards.

While fire may be seen to provide a set of selective forces for hardseededness, there have been numbers of other theories to account for the habit. Hard seeds in desert washes, for example, have been linked to the ephemeral nature of streams in these regions; when the sand and gravel in the stream beds is set in motion by water the seeds may be scarified and thereby released for germination (Went 1955). Hard seeds may also provide a mechanism for species persistence in annuals of arid lands such as the Atriplex spp. described by Beadle (1952). Softening of seed after passage through birds or other animals may place the seeds in an ideal nutritive environment for establishment. Again, the hard seedcoat may inhibit predation (Janzen 1977) while its smooth contour may prevent transport by ants in a similar way to that suggested by Pulliam and Brand (1975).

With so many selective forces operating in the determination of hardseededness, and so little study, it is not surprising that no regional generalities are possible. Indications have been given in the literature, however, for an absence of hardseededness in some areas. E. A. Johnson (1975) found a general absence of seed in forest soils of the subarctic of North America. Rizzini (1976), who worked in the fire-prone cerrado of Brazil, considered (after a study of seed germination of selected plants) that fire "seriously hinders regeneration by means of seeds." Thus, for these two areas at least there is some evidence, albeit indirect, for a lack of hardseededness in the flora.

DISCUSSION

Many aspects of the developmental patterns of plant species could be considered as adaptive to fires. Only four of these have been considered above. Other possibilities include seed burial, plant longevity, chemical composition, time to first flowering, or patterns of leaf shedding. There are many traits which may facilitate survival or reproduction during a certain succession of fires but the number here was limited to those four which could be considered as "classical" traits adaptive to fires.

"Classical" Traits Adaptive to Fires

The four broad traits chosen are those which may be observed after a single fire and it is likely that this is the reason for their being singled out in the literature. Really, the multitude of traits which comprise the life cycle of the plant may be considered adaptive.

Adaptation is the property of the life cycle, and the fire regime in all its variety is the selective force in a fire-prone environment. This became clear from the examination of the different traits above. Thus fire intensity, frequency, and season of burn were important to survival; so, too, was the type of fire (peat or aboveground fire) although this was only mentioned in passing. Timing of burning was an important factor in determining the flowering response of many plants. Seed dehiscence may be affected by fire intensity particularly if storage organs are high in trees. Seed germination may be greatly affected by fire intensity. Thus, selection for the traits examined must be thought of in relation to components of the fire regime, or various combinations of these components.

The traits examined were influenced by factors other than fires. Plant characteristics associated with survival during fire were seen to enable survival for defoliation due to many agencies, not just fire. The various mechanisms involved seemed to be associated with survival during stressful periods in general, rather than stress caused by fire occurrence in particular. For fire-stimulated flowering, the role of fire may be seen as the trigger for mast fruiting, in the same way that other species behave this way upon the command of other triggering devices. Profilic flowering could allow better fertilization, or the satiation of pre- or postdispersal predators. Fire-stimulated flowering may be a device to produce abundant seed for a fire-prepared seedbed or may allow respite from disease or allelopathic inhibition. Seed storage and subsequent seed release by fire may be seen as analogous to fire-stimulated flowering and similar selective forces may be involved. Many selective agents may select for hardseededness and the situation may be seen as analogous to that for plant survival.

Indirect Consequences of Trait Selection by Fires

The indirect consequences of selection for behavior associated with fire events could be numerous and there has been some speculation concerning these earlier in this contribution and in the literature. A few examples are mentioned below in order to stimulate thought and action in an interesting and little-studied field.

Rourke and Wiens (1977) have suggested that selection has taken place for fire survival in some Proteaceae of South Africa and Western Australia through the development of a prostrate rhizomatous habit which, in turn, "should strongly promote ground flowering." As a consequence of this, Rourke and Wiens (1977) speculated, pollination may have shifted from birds to nonflying mammals. Perhaps a similar explanation could hold for the herbaceous perennial Alexgeorgea of Western Australia; Carlquist (1976) suggested that the "underground flowering and fruiting habit" of these species was related to fire resistance.

Some of the possible interrelationship between fires, seed storage, and periodicity in flowering of Eucalyptus regnans have been suggested implicitly above. Periodicity in flowering could be important to avoid very high losses to predators, but seed storage then becomes imperative if seed supplies are to be always available at times of fire. For lodgepole pine, constancy of seed crops, seed storage, and predispersal predation of seeds could be linked. So, too, could bark thickness, mountain pine beetle attack (which is more frequent in thick bark, Amman and others 1977), serotiny, and fire regimes.

In Central America Janzen (1967) has observed swollen thorn Acacia spp. to survive fire by root suckering. If the new shoots are not colonized by ants (which live in the swollen thorns) the new sucker is subject to "many mortality factors" including defoliation by insects. In addition to direct defense of the plant from insect herbivores, the ants clear an area around the base of the plant which effectively reduces shade from competitors and apparently reduces the rate of insect invasion. Also, it reduces the chances of shoot death by fire. It is perhaps noteworthy that those other acacias of the region which are not associated with ants have a thicker bark and "appear to be more fire hardy."

SUMMARY

Four traits considered adaptive to fires have been examined. For each trait, examples could be found from environments subject to a wide variety of fire regimes. One reason for this could be that the traits selected have been associated with the occurrence of individual fires, whereas the species which display them adapt to particular combinations of fire occurrences.

Each trait examined revealed considerable variation and appeared to be under genetic control. Fires were shown to affect this variation in a number of ways reflected in the plant's survival or reproduction.

The many traits enhancing survival during fires may also enhance survival during stress from other environmental factors. In some cases, such as the tufted crown of some arborescent monocotyledons, the trait appeared to be a preadaptation to fires rather than a consequence of fire selection because it may occur in a fire-free environment. Prolific flowering occurred in examples where fire was an important trigger, and where it was not, thereby suggesting that the more general phenomenon was the flowering behavior rather than fire occurrence. This does not mean that fire was unimportant where it did trigger the response; it was. Seed storage on the plant produced a similar result to that of fire-stimulated flowering in that fire triggered the events leading to large accessions of seed to the soil. Seed stored in the soil may be released for germination by fire but also by many other environmental agencies associated with particular sites.

CONCLUSIONS

The four adaptive traits chosen for discussion provide interesting examples of selection by fire regimes and may be seen as part of the process of selection for particular life cycles. There is wide scope for further work in understanding the interactions between fire regimes, other physical site variables, and fauna (including insects) in selecting for particular traits. With broader ecological study of traits and life cycles in a fire context, a more integrated understanding of landscapes should emerge.

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REPRODUCTIVE CYCLES AND FIRE REGIMES

Jon E. Keeley

Assistant Professor
Department of Biology
Occidental College
Los Angeles, Calif.

ABSTRACT

An understanding of the evolutionary role of fire in ecosystem development requires knowledge of life history characteristics. Fire frequency plays an important role in determining the specific reproductive modes possible for a given environment. Since natural fires are randomly distributed in space and time, often a more important focal point than response to the modal fire frequency will be species' resilience to the range in fire frequencies encountered. Failure to appreciate species-specific differences in resilience in managing natural ecosystems can spell extinction for some species. A component of the fire regime particularly important to the evolution of reproductive strategies is the pattern of burning, i.e., patchy vs. extensive. Oftentimes a whole suite of characteristics will be associated with one pattern or the other. In some instances, a suite of characteristics may be common across all growth forms. More often, different growth forms carry with them a unique set of potentialities and limitations with respect to resilience to fire.

KEYWORDS: life histories, r and K selection, resilience

INTRODUCTION

Emergent properties of ecosystems cannot be explained mechanistically without a clear understanding of population level phenomena. Thus, understanding fire's role in ecosystem development requires knowledge of the component species' life history attributes.

Life Histories and Growth Forms

A generalized life history of a plant population resembles that in figure 1a. We can distinguish an r-phase where the population is growing at or close to the maximum

possible (close to intrinsic rate of increase r) and a K-phase where population growth is zero (close to carrying capacity K). Not all populations have a senescence phase and in fact we can distinguish extremes in this respect (compare curves 1 and 2, fig. 1b). Different environments produce conditions which tend to favor a No. 1 or No. 2 type life history. The important environmental parameter is disturbance; No. 1 life history being favored in frequently disturbed environments, No. 2 in infrequently disturbed environments.

McArthur and Wilson (1967) described these respective environmental types as imposing r -selection (No. 1) or K -selection (No. 2), though as pointed out by Gadgil and Solbrig (1972) these are purely relative terms and no species is entirely r - or K -selected. Pianka (1970) attempted to define life history attributes of r -selected vs. K -selected species. According to Pianka, the former should have rapid development, small body size, early reproduction, and a high intrinsic rate of increase relative to K -selected species. Although this has provided a useful framework for life-history studies, there is abundant evidence that one must be cognizant of the particular ecology in order to predict attributes of organisms subjected to r - or K -selection (Wilbur, Tinkle, and Collins 1974).

One generalization concerning plant responses would be that growth form could be aligned along an r - K gradient with herbs at the r -end and trees at the K -end. While herbs could be favored for reasons other than r -selection, e.g., high winds could select for a low-growth habit, in the main this is probably a valid generalization. Thus, the frequency of a disturbance, e.g., fire, can select for different life histories and, as a consequence, different growth forms. It follows that the reproductive mode, i.e., those life cycle parameters which are immediately responsible for the continuance of the population through time, should be greatly influenced by differing fire frequencies.

Reproductive Cycles

It has recently been suggested (Harper 1977) that the term "reproduction" be restructured in usage to mean production of a new individual from a single cell, usually a zygote. Harper argues that what is termed "vegetative reproduction" is merely growth in a horizontal plane. However, the outcome of such "growth" may be identical to (apomictic) seed "reproduction," and unlike growth in a vertical plane, viz, production of new individuals distinct from the original plant. Janzen (1977) has perhaps suggested one solution to this problem by arguing that apomictic seed production be viewed as lateral growth. The purpose in making such a distinction

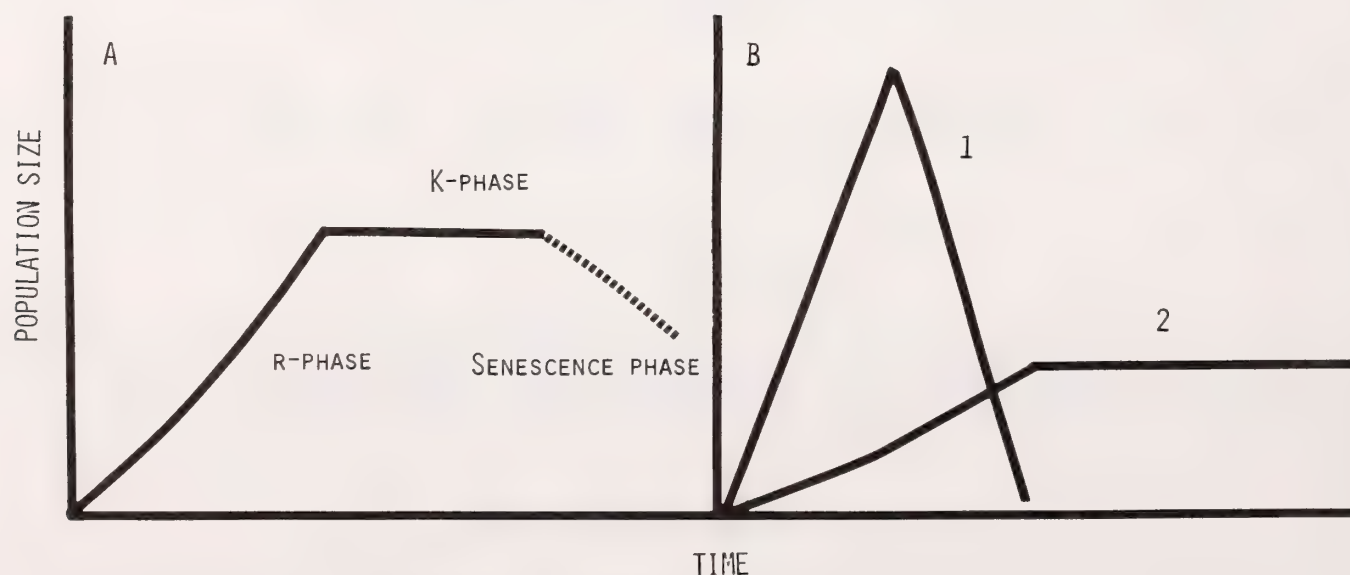


Figure 1.--(a) Generalized life history of a plant population, (b) life histories representing extremes with respect to population senescence.

is to emphasize the genetic identity of these offspring. The importance of such a distinction, in terms of r- or K-selection, is at least questionable in light of recent discoveries of abundant genetic diversity in many asexually reproducing populations.

In this discussion I will use reproduction in a more conventional sense and perhaps more broadly as "to produce again" (first definition, Webster's Collegiate Dictionary 1969). Thus, in the present discussion, the components of a reproductive cycle are those adaptations directly responsible for population recovery following destruction by fire. I will distinguish between "reproduction" and "regeneration." The former includes any lateral spread with the potential for producing "new individuals," either seed or vegetative reproduction. Regeneration will refer to the production of an individual in situ once it has been largely destroyed (e.g., resprouts from the stem or underground parts), see table 1.

The particular reproductive strategy (where strategy is the predetermined genetic component of the life cycle, after Harper and Ogden 1970) will include, to differing extents, both "reproduction" and "regeneration." It should be recognized that the basic genotypic program, or strategy, may include a range of possible developmental pathways dependent upon environmental conditions.

TABLE 1.--Reproductive and regenerative options in the reproductive cycle of plants

Reproduction		Regeneration	
Seed ^{1/}	Vegetative	From below-ground parts	From aboveground parts
Disperse	"Runners" above and below ground	Resprouts from stem or roots	Resprouts from epicormic buds
Remain <u>in situ</u> in the soil	Layering		
Remain <u>in situ</u> on the plant	Gradual spread by repeated resprouting from basal parts		

^{1/} Sexual and asexual.

GROWTH FORM, REPRODUCTIVE MODE, AND FIRE REGIME

Particular growth forms and reproductive modes have evidently evolved in response to fire in many parts of the world, thus a wide array of plant communities have been labeled "fire adapted." In order to understand the evolution of these features we must consider the influence of fire per se, but also the components of a fire regime. Gill (1973) distinguishes three components: fire frequency, fire intensity, and season. Fire frequency plays a dominant role in determining vegetation structure and vegetation structure largely determines fire intensity.

In addition to being an important determinant of growth form, fire frequency may play an important role in determining reproductive strategies. The objective here is to evaluate the effect of fire frequency on reproductive strategies. The focus of this paper will not be to document the effect of fire on reproductive strategies of plants from all ecosystems; rather, selected systems will be emphasized. My approach will be to compare major vegetation types in which a particular growth-form dominates, viz, herbs, shrubs, trees, across the range of fire frequencies represented.

Several difficulties will be evident throughout. One, we have very incomplete knowledge of natural fire frequencies for most regions. As a consequence, the basis for ranking communities by fire frequency will be rough estimates based in large part on considerations discussed in the next section.

A second problem is that the preponderance of fire-ecology studies have been community level and thus there is a dearth of information on the population biology of most fire-type species. It is hoped that this report will illustrate the dynamics of postfire recovery and how little community-level indices tell about these processes.

A third difficulty is that fire is a natural disturbance with effects similar to other disturbances, e.g., frost, drought, blowdowns, tornadoes, heavy snowpacks, animal grazing, etc. Thus an underground stem may allow a woody plant to recover after a tornado or a fire. Likewise, thick bark may act as a barrier to dessication as well as fire damage. To evaluate the evolutionary effect of fire frequency on reproductive strategies, one must separate the selective influence of other environmental parameters. This, however, is not always possible.

Finally, one must distinguish between fire regimes which have a selective effect on plants, and those that do not. Harper (1977) distinguishes disasters from catastrophes; the latter being disturbances that do not occur frequently enough to be of any selective influence on the life cycle, e.g., to make a case that fire has played an evolutionary role in the Hawaiian flora, one must do more than demonstrate that wildfires can occur on occasion (cf. Vogl 1970).

Fire Frequency

Simplistically, fire frequency is determined by the frequency of ignitions concomitant with a "low" moisture content of the vegetation. A "natural" fire frequency is determined by the frequency of lightning and degree of aridity in a given environment. Since both of these parameters vary seasonally, the degree to which they coincide is important. Given "adequate" burning conditions, "natural" fire frequency should be a monotonic function of lightning frequency. On the other hand, fire frequency increases with aridity only to the point where increasing aridity results in insufficient biomass to carry a fire.

At present man plays a dominant role in determining fire frequency. On one hand he provides ignition for many wildfires (frequently during the driest season); on the other hand he puts out many "natural" as well as manmade wildfires. Whether the net effect is to increase or decrease the "natural" fire frequency is debatable and probably varies with the ecosystem.

Before proceeding, a word about the distinction between "natural" and "manmade" fire frequency is in order. "Natural" must be considered in context. To a sociologist, a natural fire frequency source may include modern man. To the U.S. Park Service (largely committed to the preservation of resources as they were at the time they came under its jurisdiction) natural fire frequency sources include aboriginal but not modern man. In the present discussion, "natural" is being used in an evolutionary context, i.e., the environment which has selected for reproductive strategies. It is assumed that relatively recent changes in fire frequency, e.g., due to aboriginal burning in North America, have tended to affect species distributions more than species adaptations. Potentially, this is less true in the Old World (with longer human influence) and where adaptations are under simple genetic control, e.g., serotiny in jack pine (Teich 1970).

Fire frequency has been defined in various ways. I suggest that the mean (arithmetic average) is not as relevant as the modal (most common) fire-free interval. Certainly, in many environments the variance and range is of more selective importance

than any measure of central tendency. Thus a species' resilience (i.e., ability to recover) to minimum and maximum fire-free intervals may be critical to its survival.

HERBACEOUS VEGETATION TYPES

The major herbaceous vegetation types representing a spectrum of fire frequencies are listed in table 2. Indicated also is a rough estimate of the modal fire frequency for each, based on interpretation of the available literature and evaluation of the fire climate and lightning frequency. Additionally, a suggested value for the minimum and maximum interval to which they could adjust (i.e., a measure of their resilience) is included.

TABLE 2.--Principal herbaceous vegetation types, with an estimate of their natural fire frequency and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

Vegetation type	Modal fire frequency	Minimum fire-free interval	Maximum fire-free interval
		Years	
Perennial grassland	5 - 25	0	10 - 50 (?)
Annual grassland	5 - 25	0	100 (?)
Fire florals	20 - 50	10	100 (200?)
Miscellaneous fire- tolerant species	?	1 - 2	?
Marshes	30 - 100	5	∞
Wet meadow and tundra	50 - 100	5	∞

Perennial Grasslands

Perennial grassland describes a number of plant communities in both temperate and tropical regions of the world. As the name implies, these areas are dominated by perennial grasses, though usually in association with a variety of annual grasses and herbaceous dicot species. In North America, there is an array of grassland associations (Kucera, this volume) and one can distinguish similar patterns in tropical regions (Phillips 1965). Grasslands generally have an annual period of drought coinciding with lightning storms, and occur on broad level plains or rolling hills that lend themselves well to the spread of surface fires (Daubenmire 1968, Vogl 1974). Fire plays a major role in the maintenance of many grasslands. A striking example of this is the experimental plots set up by P. V. Wells (University of Kansas) in eastern Kansas. Areas burned annually are vigorous grasslands whereas adjacent land unburnt for 15 years is largely second-growth hardwoods (personal observation, see also Bragg and Hilbert 1976). In light of this, it is not surprising that many tall grass prairie species play a dominant role in secondary succession in the East (Swan 1970). However, not all grasslands are fire dependent. Those on deep soils in regions subjected to occasional severe drought are generally not invaded by woody plants, even in the absence of fire (Weaver and Albertson 1956).

The dominant grassland species in both temperate and tropical regions are hemicryptophytes; the aboveground portion dies back at least once a year (Vogl 1974, West 1971). In most species the culms are tufted or caespitose with short rhizomes. Dormant buds occur at or just below ground level and commonly are protected by closely packed persistent dead leaves and leaf sheaths (Daubenmire 1968). Root systems are extensive and deep, commonly reaching depths of 2 meters (Weaver 1958). All these characteristics contribute to the ability of temperate and tropical grassland species to withstand intense grazing, frosts, and annual dry periods as well as severe periodic droughts (Albertson and others 1957, Weaver and Albertson 1956). Longevity of grass species varies widely; even among species of similar growth form, e.g., some tussock-forming grasses are reported to reach a maximum age of 10 years (Canfield 1957) whereas other species are thought to survive over 100 years (Crampton 1974).

The seed of some species is widely dispersed. The relatively small caryopsis, large awn, and persistent pappus-like hairs in some species (e.g., Andropogon) contribute to their ability to invade recently burned areas. Other species (e.g., Sporobolus), with different caryopsis characteristics, are seldom invasive into recent burns (Hodgkins 1958). Seed storage in the soil by perennial grass species is generally low to nonexistent (Lippert and Hopkins 1950, Major and Pyott 1966). This probably stems from a lack of soil carryover from year to year as well as erratic annual seed production. Apparently seedling establishment is an uncommon event (Hanson 1950).

Vegetative reproduction in perennial grasses is generally limited to production of small clumps or tussocks. This can, over long periods of time, lead to the formation of widely separated tussocks (Harberd 1967). Vigorous vegetative reproduction, through either stolons or rhizomes, is generally lacking. Under a frequent fire regime, such structures may be a liability since their proximity to the soil surface would mean greater losses to the plant (McLean 1969). There are, however, a variety of cost-benefit arguments for the presence or absence of stolons and runners.

Regeneration from basal buds following destruction of aboveground parts is well developed in most perennial grassland species. Commonly accompanying regeneration is an increase in seed production (Hadley and Kieckhefer 1963, West 1971, Vogl 1974). This probably results in seed production at a time of enhanced seedbed conditions. Undoubtedly, such a scenario would be affected by the season of the fire, particularly in temperate grasslands composed of mixtures of late-spring flowering C_3 grasses and late-summer flowering C_4 grasses. In North America lightning fires are concentrated between spring and summer (Komarek 1967, Barden and Woods 1973) with burning conditions beginning in the spring in the more southerly localities and later, northward. Cool season C_3 plants in southerly locations may have a higher probability of flowering as well as being in a more vulnerable phenological state at time of burning than late-flowering species. Warm season C_4 plants in southerly localities would be most resistant to spring fires since growth would be beginning, and afterwards they would be safe from fire for at least a year. Northward, fires would be later in the summer, after C_3 grasses had dispersed their seeds and at the time of C_4 grass flowering. There is some evidence to support this (Daubenmire 1968, Zedler and Loucks 1969, Rice and Parenti 1978).

Several factors affect the extent of postfire regeneration. Under annual burning, annual grasses and herbs commonly increase at the expense of perennial grasses (Pickford 1932, Kennan 1971, Smith and Owensby 1972). This is most marked under a natural regime of summer fires (Bragg 1978) since the perennial rootstocks suffer greater destruction (Garren 1943, Daubenmire 1968). Increased numbers of annuals also occur after severe drought (Weaver and Albertson 1956) and in both cases are probably related to increased open space for seedling establishment. In the absence of disturbance such species often are restricted to refugia created by extreme edaphic conditions.

Herbaceous dicot species common to grassland communities represent a variety of families and life histories, although mainly geophytes and hemicryptophytes. Seed production is annually more consistent among these broad-leaved herbs than in perennial grasses. Seed dispersal is via wind or animals. There is apparently little seed carryover from year to year except during prolonged droughts (Weaver and Albertson 1956). A few legume species, from frequently burned areas in the southeastern U.S., have seeds which demonstrate enhanced germination when exposed briefly to high temperatures ($80^{\circ} - 90^{\circ}\text{C}$), though there is considerable germination without any heat treatment (Martin and others 1975). Some species spread both by seed and stolons or rhizomes, proportions varying with fire frequency. For example, wild strawberry (*Fragaria* sp.) invades recently disturbed sites via seeds, and once established spreads locally by stolons as well as producing seeds for more distal establishment. As the community becomes crowded, and probability of fire increases, stolons (which survive fires very poorly, McLean 1969) are produced less frequently (Holler and Abrahamson 1977).

Many herbaceous dicots can survive fires via underground parts which regenerate. The extent to which an individual can survive fire is closely tied to the depth of underground parts and thus one finds inter- and intraspecific variability in regeneration. A good example of prairie forbs capable of regenerating after fire is species of *Liatris* found throughout the midwestern and eastern portions of the U.S. Some can live perhaps 40 years (Levin 1973), and it is the older individuals with larger, deeper corms which are the most resistant to fire. Schall (1978) examined the age-structure of a population of *L. acidola* 2 years after fire in a mature prairie of southeast Texas. Her results (fig. 2A) suggest that many of the plants 1 to 3 years of age at the time of fire were killed, and following fire there was a flush of new seedlings. Thus, the population cost of fire for *L. acidola* is a loss of juveniles but the benefit is a surge of new seedlings. Benefits may outweigh costs in the life history of *Liatris* since Kerster (1968) has found that older midwestern populations of *L. aspera*, in the absence of disturbance, stop recruiting new individuals into the population (fig. 2B). Periodic fires may rejuvenate older populations. It is apparent from figure 2A that too frequent fires would be detrimental to *Liatris* populations as is true for other perennial forbs (Pickford 1932).

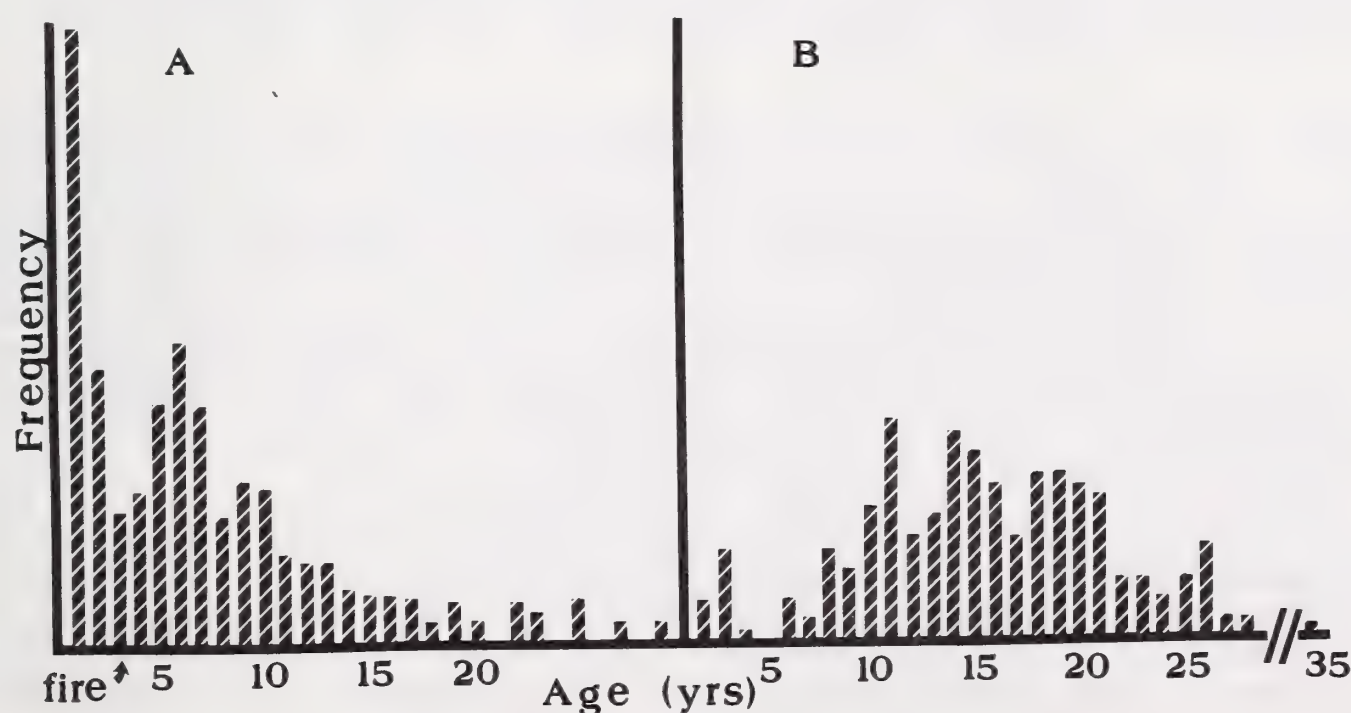


Figure 2.--(A) Age structure of a *Liatris acidola* population of 2 years after fire (redrawn from Schall 1978). (B) Age-structure of *Liatris aspera* population in the absence of disturbance (redrawn from Kerster 1968). Werner (1978) has demonstrated that there is a great deal of error associated with assigning ages in *Liatris*, though Levin and Kerster (1978) claim the ages are certain for plants under 5 years.

Extensive annual grasslands are found mainly in Mediterranean climatic regions and are the result of disturbance (too frequent fires, severe drought, intensive grazing; any one or all). In California they occupy extensive portions of the Central Valley and Coast Ranges, having developed during the last 150 years from nonnative annual grasses and forbs. Clements (1920) proposed that the annual grassland replaced a pristine bunchgrass community after intensive grazing, coupled with drought. This view was based on the presence of small isolated populations of native bunchgrass assumed to be "relicts" and is considered by some to be true "beyond all doubt" (Heady 1977). However, Cooper (1922) argued that woody vegetation is climax in coastal valleys of California but has been replaced by grasslands due to repeated fires by man. Naveh (1967) invokes a similar scenario to explain the origin of annual grasslands in Israel (the origin of California's annual grass species). This theory is based on assumed "relicts" of chaparral within grasslands as well as historical documentation of chaparral replacement by grassland. In all likelihood, annual grasslands were derived both from perennial grasslands, particularly on deep clay soils, and (extensively) from woody vegetation on shallow rocky soils (Wells 1962). Increased fire frequency due to human exploitation is thought by Wells (1962) to be a major factor in their origin in the Coast Ranges of California.

Present fire frequency in annual grassland probably varies from annual fires to 50 or more years between fires. Despite the likelihood that annual grasslands in many situations owe their origin to frequent fires, there is little evidence that annual grasslands require frequent fire for maintenance. Perennial bunchgrasses invade annual grasslands very slowly (White 1966b), and the low vagility of chaparral seeds makes invasion of grassland by chaparral a threat only along narrow ecotones between the two vegetations (Schultz and others 1955, Biswell and Street 1948). Coastal sage species on the other hand have well-developed colonizing ability (Wells 1962) and when juxtaposed with grassland they can replace it in less than 15 years without fire (Westman 1976). Considering the broad expanse of many of these grasslands (and thus lack of an invading seed source) they are probably stable for long periods without fire. White (1966a) describes an oak-grassland area in the coast ranges which has remained stable more than 25 years without fire.

The dominant plants are annual grasses and forbs; most are natives of the Mediterranean region. Seed germination occurs late in fall following the first rains, with much of the growth occurring in winter and early spring. Flowering and fruiting are completed by early summer. Like other annual "weeds" these species are quite plastic in growth and phenology; in wet years they reach much greater sizes with larger seed production. Most species are highly r-selected for rapid germination and growth rates, small stature, and a large proportion of energy allocated to reproduction. Additionally, most possess typical colonizer attributes (viz, large numbers of small, widely dispersed seeds) and thus are ruderals in other than Mediterranean-climatic regions.

All species can tolerate frequent fires, largely because of sizable seed pools in the soil (Major and Pyott 1966), efficient means of burying seeds, e.g., hygroscopic awns (Naveh 1974), and the comparatively low temperatures of grass fires, which result in high seed survival (Daubenmire 1968). Annual grass species, however, are not well suited to annual fires. Smith (1970) found a 70 to 80 percent reduction in grass density the first year after fire and found that it took 3 years to reach prefire levels. In general, annual fires tend to favor forbs over grasses (Hervey 1949, Smith 1970). In some cases this may derive from slightly later flowering and fruiting by the grasses, which translates into a greater chance of seeds being attached to culms at the time of the fire, where temperatures are higher than at ground level (Daubenmire 1968). Also, the rosette growth form of the dominant forbs may enforce a greater spacing of individuals and thus lower burning temperatures in the seed-rain shadow. Additionally, since grasses are favored by a different set of growing conditions (Pitt and Heady 1978), fire may change the following season's growing conditions to favor forbs.

Fire Floras

In some Mediterranean-climate regions of the world there are herb floras which have a life cycle closely linked to fire. Mainly the herbs exist only as dormant seeds in the mature scrub which is "climax" for the entire region. Except in isolated openings, no seeds germinate until fire removes the shrub cover, at which time there is a proliferation of many herbaceous monocot and dicot species. Among the Mediterranean areas of the world there are regional differences, e.g., in California the postfire herb flora is predominantly annuals, whereas in South Africa it is mostly geophytes, and in Chile there is no such flora (Keeley and Johnson 1977). Of the Mediterranean fire floras, California's is best understood, thus I will focus on this region.

Germination of the postfire herbs begins after the first winter rains following a chaparral fire. Flowering begins in early spring and fruitification is completed by late spring. The majority of species are annual dicots and will not be present the second year after fire.^{1/} In order to germinate, the seeds require seed coat scarification, which comes in the next fire, presumably as intense heat, although this has not been convincingly demonstrated for many "fire-type" annuals (cf. Sampson 1944, Went and others 1952, Sweeny 1956, Christensen and Muller 1975) and other mechanisms have been proposed (Wicklow 1977).

The seeds appear to be quite long-lived, as evidenced by the proliferation of "fire-type" annuals after fires in very old (ca. 90-year) chaparral (personal observation). Undoubtedly, seed viability does decline in stands unburned for long periods of time; however, there is no information on the maximum fire-free interval they can withstand. On the other hand, the fire flora is sensitive to too frequent fires. Chaparral stands burned at several-year intervals are readily converted to annual grassland with elimination of native fire annual species. This is probably because the annual fire flora species do not compete well against aggressive annual grass species (Corbett and Green 1965). This is not surprising in light of the observation that the density of the fire-type annual vegetation is at least an order of magnitude less than the density of annual grasslands (cf. Sampson 1944, Horton and Kraebel 1955, Heady 1958, Smith 1970).

Miscellaneous Fire-Tolerant Species

There are a number of herbaceous species not easily classified into any single community but which proliferate after fire. Epilobium angustifolium is a common fire follower in a variety of habitats throughout the higher latitudes of the Northern Hemisphere. It is a perennial which produces an abundance of small, widely dispersed comose seeds that quickly invade clearings caused by fire or other disturbances. Once established, an individual can spread over an area through vigorous rhizome production. It is eventually crowded out by later successional species and thus is dependent upon dispersing to new disturbances (Ahlgren 1960). Little information is available on the effect of fires on established populations. The proximity of rhizomes to the soil surface suggests they would not survive severe fire very well (McLean 1969). Although seeds have been found in mature forest soil (Karpov 1960 cited in Major and Pyott 1966) it is not known whether they survive fire. The architecture of the diaspore indicates they are primarily adapted to colonizing after fire or other disturbances and Salisbury (1942) states that they only establish on open sites.

Another fire-following species is Pteridium aquilinum. It resembles Epilobium in that it is a widespread species producing a proliferation of dissemminules which invade recently burned sites, then spread vegetatively (Salisbury 1942, Oinonen 1967 cited in Harper 1977). Repeated fires, however, are less damaging to Pteridium because

^{1/} Keeley, S. C., J. E. Keeley, S. Hutchinson, and A. W. Johnson. Post fire succession of the herbaceous flora in the southern California chaparral. Unpublished ms.

the rhizomes are deep enough to survive high temperatures (Flinn and Wien 1977). Several other species have a similar life cycle, e.g., Equisetum sylvaticum in Canada (Beasleigh and Yarranton 1974), Pteridium caudatum in Venezuela, and Gleichenia spp. in New Guinea (Gillison 1969).

Marshes

As used here, marshes refers to herbaceous communities in standing water much of the year. The chance of fire in any given year is low due to the moisture conditions of the vegetation. Periodically, however, severe droughts will cause a drastic drop in water table and produce conditions suitable for burning. Thus, in large part, fire frequency depends on local water table patterns.

The marsh dominants are perennial grasslike species from a variety of monocot families (e.g., Cyperaceae, Poaceae, Typhaceae, Juncaceae, etc.). Dependent upon the latitude, tillers emerge between spring and early summer. Not all tillers flower in a given year; e.g., Carex lacustris and C. rostrata produce tillers which commonly overwinter and flower in their second year then die (Bernard 1976). Most seeds are buoyant and dispersed to some extent by water. In fact, the marsh grass Paspalum has boat-shaped spikelets well adapted for water transport (Crampton 1974). If the study by van der Valk and Davis (1978) is typical, the soil seed pool of freshwater marshes is of considerable size. Seed of emergent species remain dormant until water levels drop and the seeds are exposed. This is also when fires are most likely to occur; thus frequent fires would not be conducive to reproduction.

Characteristic of most marsh species is a well-developed capacity for vigorous vegetative reproduction. Such stolons or "creeping" or "branching" rhizomes commonly reach several meters and more. Regeneration after fire is highly sensitive to fire temperatures. Garren (1943) states that marsh species are killed by dry-season fires because roots near the soil surface are destroyed.

In general it would seem that most marsh species are sensitive to fire due to its coincidence with seedling establishment and the high probability of destruction of below-ground regenerative parts. Nonetheless, marshes throughout the southeastern United States (and other regions of the world) are subject to severe droughts coinciding with lightning ignitions approximately every 30 to 100 years. The outcome of these periodic fires is on one hand to reduce encroaching woody vegetation but on the other hand to destroy marsh vegetation and replace it with submerged aquatics (Cypert 1972).

Wet Meadows and Tundra

This group includes a heterogeneous collection of plant associations, with the major distinction being that they occupy sites which are moist most of the year. Certain "meadows" occupying drier sites, particularly at lower elevations or latitudes, are structurally similar to what has been discussed as "grasslands." There is also a certain amount of overlap between meadow vegetation and the herbaceous component of adjacent woodlands. Meadows and tundra are extensively developed at high elevations and latitudes. The more or less perennially wet character of the vegetation makes fires of infrequent occurrence and questionable selective importance.

The vast majority of species are perennial; commonly grasses and sedges. The conspicuous absence of annuals may be related to the "closed" nature of the vegetation, i.e., lacking openings for seedling establishment. Many species reproduce sexually infrequently (Salisbury 1942), and this is reflected in small seed pools in the soil (Major and Pyott 1966) and rarity of seedlings (Callaghan and Collins 1976, Callaghan 1976), even after occasional fires (Wein and Bliss 1973). Most species are vigorous vegetative reproducers, either through creeping or branching rhizomes, stolons, or layering. These species can regenerate after the tops are removed, though fires (except when the soil is quite moist) would be damaging since roots and other regenerative parts occur near the surface.

The heavy dependence on vegetative rather than seed reproduction may result from several factors. Salisbury (1942) suggests that lower temperatures at high elevations or latitudes, or lower light levels in woodlands, are not conducive to seed production which is physiologically more demanding. Alternatively, extreme conditions could make vegetative reproduction a safer gamble due to the much greater food reserves available; theoretically, seeds could evolve large reserves, though this may be too risky an investment in an environment where seed crop failures are common and unpredictable. Vegetative reproduction also has greater flexibility in initiating and arresting itself, unlike a germinating seed which is committed to a certain increment of growth before arresting development; a potentially important factor in an unpredictably "extreme" environment. Finally, moist conditions and lack of frequent disturbance, leading to a "closed" community with few openings, is a poor environment for seedling establishment, particularly ones with minimal food reserves (Thomas and Dale 1975).

Summary: Herbaceous Vegetation Types

The dominant strategy for surviving in a frequently burned perennial-type grassland is that of a long-lived perennial which, through its capacity to resprout from below-ground parts, appropriates space and holds it for extended periods. Certainly fire is only one aspect of the grassland environment which has selected for this strategy. The intensive selective pressure of droughts is suggested by the extensively developed root systems of most grassland species (occasionally reaching depths of 4 m or more, Weaver 1958). Perhaps to insure some colonizing ability (e.g., into areas subjected to severe drought, intensive grazing, badger building, tornadoes, or fire) seeds of the perennial grassland species are light; consequently they require "openings" in which to become established. In grasslands unburned for extended periods of time, openings may be rare and consequently seedling establishment is also rare. Under long fire-free periods, populations of some species may go extinct although most species are resilient to periods of low fire frequency as well as periods of high fire frequency. The extent to which perennial grasslands are dependent upon frequent fire is related to proximity and invasiveness of woody vegetation.

Mediterranean-climate annual grasslands represent one of the most fire-resilient herb communities; existing under frequent as well as infrequent fires. These annual species demonstrate few specific adaptations to fire per se. They have r-selected attributes and are species adapted to rapid colonization. Although most r-selected species require frequent disturbance to remove invading and more competitive K-selected species, such is not the case for these annual grassland species. Once the original vegetation has been removed, reinvasion is imperceptibly slow and thus r-selected species remain dominant with or without additional disturbance.

The fire-type annual floras of certain Mediterranean regions exhibit the greatest degree of adaptation (specifically) to fire. These species are specialized r-strategists with rapid establishment from stored seed "only" in response to fire; however, they are not good colonizers, perhaps because disturbances are generally widespread. They are not resilient to very frequent fires (return of the shrub cover is required to shade out other more aggressive herb species) but can withstand fire-free periods as long as a century. Thus, fire-type annuals illustrate that specialized adaptations to fire do not necessarily imply adaptation to frequent fires.

Epilobium and Pteridium illustrate strategies adapted to periodic intense fires which do not destroy the parent population but open up nearby areas. Abundant light, wind-dispersed disseminules are well adapted to broadcast colonization of denuded sites, even at some distance from the parent population. It should be recognized, however, that these species are not dependent on fire since they commonly colonize sites opened up by other types of disturbance.

Species common to most marshes, meadows, and tundras appear to be poorly adapted to fire and not resilient to frequent fires. They differ from more fire-adapted communities in that reproduction is predominantly from stolons and shallow rhizomes, structures easily destroyed by fire. Although these three communities can recover from fire, its effect is probably more that of a catastrophe (*sensu* Harper 1977) in that the selective consequence is to decrease "short-term fitness."

SHRUB VEGETATION TYPES

The major shrub vegetation types to be considered represent adaptive responses across a spectrum of fire frequencies (table 3).

Mediterranean-Climate Evergreen Scrub

The five regions of the world characterized by a cool-winter-rain, hot-summer-drought climate are dominated by a vegetation of closely spaced evergreen shrubs with heavily sclerified leaves. In most of these regions summer droughts are occasionally interrupted by thunderstorm activity resulting in lightning fires carried far by the dense continuous brush cover. Although the five Mediterranean regions are broadly similar there are significant differences. I will focus in detail on the California chaparral since the life histories of these shrubs (coupled with associated trees, see later section) illustrate that species in a fire-type community represent a variety of optima and resiliences to varying fire frequencies.

TABLE 3.--Principal shrub vegetation types, estimated natural fire frequency, and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

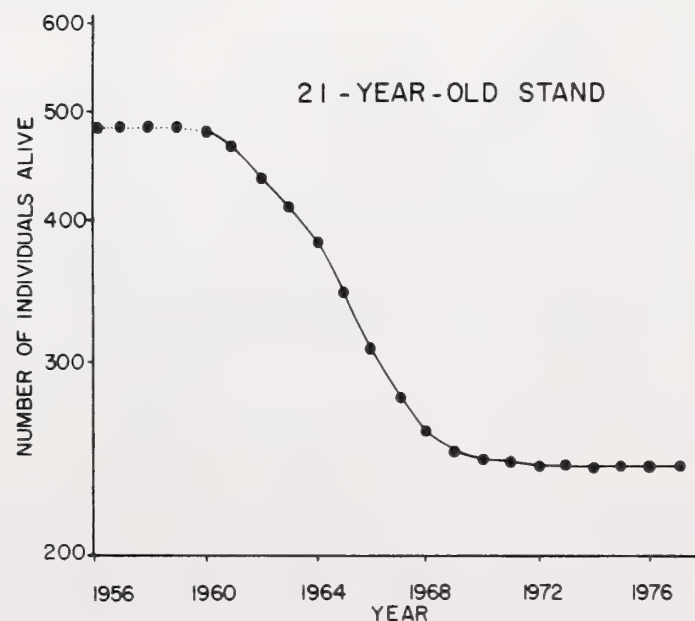
Vegetation type	Modal fire frequency	Resilience	
		Minimum fire-free interval	Maximum fire-free interval
		<u>Years</u>	
Mediterranean-climate			
evergreen scrub	20 - 50	10	100-200 (?)
Mediterranean-climate			
deciduous scrub	30 -100	10	100(150?)
Humid evergreen scrub	20 - 30	2 - 5	200 (?)
Arid (desert scrub)	50 -100	10 - 20	(?)
Temperate forest			
successional shrubs:			
Western forest shrubs	20 -100	5	300-400 (?)
Eastern forest shrubs	100 -500	5	∞
Scrub steppe	100 -300	30	∞
Tropical rain forest			
understory shrubs	∞	∞	∞

California chaparral consists of shrubs 1.5 to 3 m tall almost always occurring in stands with an (aboveground) even-age structure (excepting one anomalous shrub, Yucca whipplei). These stands are distributed in a mosaic determined by burning patterns. Presently nearly all of the acreage burned in southern California results from manmade fires (Keeley 1977b). As a consequence fire frequencies vary with proximity to habitations; e.g., fires occur every 2 to 5 years in some heavily used foothills of the San Gabriel Mountains overlooking Los Angeles whereas large portions of the little-used Santa Ana Mountains have never had a recorded fire (USDA For. Serv., unpublished data). The commonly accepted modal frequency of natural fires is 20 to 30 years. Undoubtedly in prehistoric times this varied widely dependent upon elevation and proximity to the coast (Keeley 1977b, Byrne and others 1977).

Chaparral shrubs represent a variety of plant families and life histories. Some species, e.g., Heteromeles arbutifolia, Cercocarpus betuloides, Rhus laurina, and Rhus ovata, are capable of great longevity (100-200 years?) becoming small trees in isolated localities. Others, in particular Ceanothus species, are traditionally considered short-lived (40-60 years), although their longevity is closely tied to stand structure. As shown by Schlesinger and Gill (1978), as the canopy closes in "pure" stands of Ceanothus megacarpus, there is a sudden die-off (fig. 3) presumably due to rapidly increasing competition for light. In older mixed stands, mortality of Ceanothus greggii is apparently constant (Keeley and Zedler 1978) and probably reflects gradually increasing competition for light and soil moisture in this shade-sensitive shallow-rooted species. Thus, if these "short-lived" species escape close competition they can be quite long lived (Keeley 1975, Schlesinger and Gill 1978).

Seed production fluctuates widely from year to year dependent in large part on precipitation patterns. Some species initiate flower buds the year prior to flowering, whereas others do not; thus, seed production is not usually synchronous across species (Keeley 1977a). There is little indication that seed production declines with age, and in one study (Arctostaphylos glauca) seed production was much greater in 90-year-old shrubs than 20-year-old ones (Keeley and Keeley 1977; a similar pattern was found for Adenostoma fasciculatum, Keeley and Keeley unpublished data). Seed dispersal modes vary widely, e.g., the chaparral shrub, Adenostoma fasciculatum produces an abundance of light seeds; however, they are not highly specialized for (and chaparral is not conducive to) wind dispersal and probably are not dispersed widely. Ceanothus and Arctostaphylos species are important chaparral constituents with, for the most part, localized seed dispersal. Quercus dumosa is a common chaparral shrub characterized by erratic production of large acorns potentially widely dispersed but heavily preyed upon. A number of quantitatively minor species, e.g., Heteromeles arbutifolia and Rhamnus crocea, have fleshy fruits which are probably widely dispersed by birds.

Figure 3.--Density of live Ceanothus megacarpus shrubs after fire in 1955 (from Schlesinger and Gill 1978, with permission of Duke Univ. Press., copyright by the Ecological Society of America).



Seed storage in the soil is variable. The most common species, Adenostoma, Ceanothus, and Arctostaphylos, have a seed-coat scarification requirement usually met by intense heat during fire (Stone and Juhren 1953, Quick 1935, Hadley 1961, Berg 1974). Other species such as Quercus dumosa, Rhamnus crocea, Heteromeles arbutifolia, and Prunus illicifolia have no such scarification requirement and will germinate readily (Mirov and Kraebel 1937, Keeley unpublished data). Consequently, seedlings of these species occasionally establish in mature chaparral; Patric and Hanes (1964) recorded several hundred per hectare in very old chaparral. It is doubtful whether these contribute to the mature canopy since they are usually stunted (Patric and Hanes 1964) and many eventually die, in part, from overgrazing by small mammals (Keeley 1973, Horton and Wright 1945). Thus these shrub seedlings seldom establish under mature chaparral or in openings created by dead shrubs (Hanes 1977). Following fire, there is an abundance of seedlings of Adenostoma fasciculatum and certain species of Ceanothus and Arctostaphylos, all from soil-stored seed, germinating in the first postfire year. Postfire seedling establishment of other species is sporadic and often insignificant numerically (Zedler 1977a).

The capacity to resprout from basal parts after fire is widespread in chaparral shrubs, being found in all species except the majority of Ceanothus and Arctostaphylos species. The species which can resprout after fire vary in the proportion of the population which actually survives to do so. Thus, postfire regeneration is either by seedlings from soil-stored seed or resprouts from basal vegetative parts or both. The dependence upon seedlings or resprouts varies from species to species. We can picture this schematically in figure 4 where a point along the abscissa, corresponding to a particular proportion of seedlings vs. proportion of resprouts, describes the reproductive tactic. However, this position will vary spatially (from population to population) and temporally (from one fire to the next); thus a species is best characterized by a reproductive strategy which occupies a region along the abscissa. For example, Quercus dumosa is a vigorous resprouter but seldom establishes seedlings, thus its reproductive strategy is represented by region "a" along the abscissa. The ubiquitous Adenostoma fasciculatum is temporally and spatially quite variable in post-fire resprouting and thus might be described by region "c." There is one significant exception to this pattern; the majority of Ceanothus and Arctostaphylos species do not occupy a region along the abscissa but rather a single point (see the arrow, fig. 4). These species are totally incapable of resprouting under any condition and thus are entirely dependent upon seedling production for postfire regeneration.

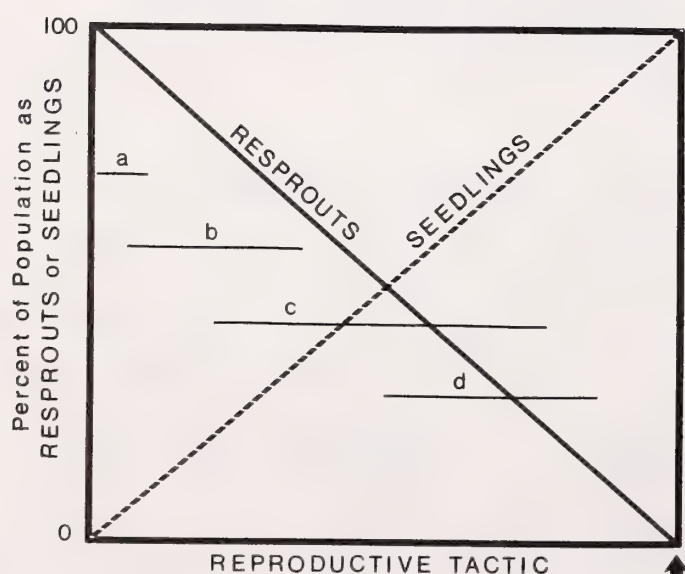


Figure 4.--Reproductive options available to shrubs after fire. See text for further explanation.

A summary of these characteristics is given in table 4. From this we can distinguish two modes. One group, consisting of the most abundant chaparral shrubs (Adenostoma, Ceanothus, and Arctostaphylos), is best developed on the more xeric sites and is shade intolerant. They produce more or less locally dispersed seeds which are stored in the soil until stimulated by fire to germinate. Some resprout, but others do not. The other group consisting of shrubs such as Quercus dumosa, Heteromeles arbutifolia, Rhamnus crocea, and Prunus illicifolia are best developed on the more mesic slopes. They are mostly long-lived, shade-tolerant species capable of outliving, overtopping, and shading out most of the group 1 species. They produce widely dispersed seeds which do not require fire for germination. They occasionally establish seedlings in mature chaparral, but seldom contribute seedlings to the postfire flora. All are vigorous resprouters.

TWO REPRODUCTIVE STRATEGIES

How can we account for these two different reproductive strategies? In light of modal fire frequency of every 20 to 30 years, the group 1 strategy is easily rationalized: Produce seeds cued to germinate only after the next fire, since (1) seedlings would be unlikely to establish in the shade of existing shrubs, (2) seedlings are likely to be eaten by herbivores, (3) another fire is likely to occur before the mature shrubs die out, (4) because of their smaller size, these later-establishing seedlings or "saplings" would stand little chance of surviving a fire in order to resprout, and (5) the more intense fires on the more xeric sites translate into fewer resprouts and more openings for postfire seedling establishment. Also, since these fires will be quite widespread, little benefit would be derived from dispersing seeds far and wide.

The group 2 strategy is difficult to rationalize in light of frequent fires. Seed production seems to contribute little to the future population; rather, these species depend upon resprouting to maintain population levels. One could argue that perhaps these species are relicts representing an evolutionary dead end in the face of frequent fires. Although there may be some merit to this idea, another explanation might be the following: Since these species are best developed on north-facing slopes, in ravines, and other disjunct mesic sites, widely dispersed seeds would be highly adaptive (Bullock 1978). Once a seed got to one of these more mesic sites, it would be better off germinating directly because the more mesic site would mean that: (1) It is less likely to burn as frequently as a more xeric site. (This seems particularly likely when one considers the mosaic pattern of many fires [Minnich 1974], and the possibility of more infrequent fires in prehistoric times [Wells 1962, Keeley 1977b, Zedler 1977a, Burne and others 1977].) (2) More mesic slopes would mean less intense fires and thus greater postfire resprout survival which would out-compete seedlings establishing after fire. (3) Less intense fires would mean a greater chance for late-establishing understory "saplings" to survive fires and to resprout.

Data necessary to evaluate such ideas, e.g., seed dispersal distances, seedling recruitment rates in group 2 species, successional changes in very old chaparral, and natural fire frequencies, is lacking. For the most part, group 1 species seem most closely adapted to the chaparral fire cycle: (1) They are the most abundant species; (2) they produce refractory seeds dependent upon intense heat for seed-coat scarification; (3) the resprouting species in this group produce large, bulky basal burls or lignotubers, which are specialized starch-storing structures with dormant buds that give rise to resprouts after fire; and (4) many species are highly "specialized" obligate-seeding shrubs.

LIGNOTUBERS

Jepson (1916) first described basal burls on a sprouting species of Arctostaphylos and later Wieslander and Schreiber (1939) noted that the burl was not a result of sprouting but a normal development the first year. It is this distinction which most

TABLE 4.--Qualitative summary of chaparral shrub characteristics (NS = nonsprouting, S = sprouting, - = poorly developed or absent, + = well developed), see text for complete explanation

Species	Longevity	Shade tolerance	Fruit type	Dispersal	Fire-stimulated germination	Resprouting	Basal burl
<u>Adenostoma fasciculatum</u>	+	-	achene	-	++	+	++
<u>Ceanothus</u> NS spp.	-	-	capsule	-	++	-	-
S spp.	-	+	capsule	-	++	+	+
<u>Arctostaphylos</u> NS spp.	+	-	dry berry	-	++	-	-
S spp.	+	+	dry berry	-	++	++	++
<u>Rhus ovata</u>	++	++	drupe	?	++	++	-
<u>Quercus dumosa</u>	++	++	acorn	++	-	++	-
<u>Heteromeles arbutifolia</u>	++	++	pome	++	-	++	-
<u>Rhamnus crocea</u>	+	?	berry	++	-	+	-
<u>R. californica</u>	++	++	berry	++	-	++	-
<u>Cercocarpus betuloides</u>	++	?	plumose achene	++	-	++	-
<u>Prunus illicifolia</u>	++	++	drupe	++?	-	++	-

clearly separates group 1 and group 2 because some of the latter group's species, e.g., Heteromeles, will sometimes form an irregularly shaped platformlike structure after repeated resprouting. Basal burls or lignotubers are known from sprouting shrubs in other Mediterranean regions, being common in the South African fynbos (Kruger 1977), but most highly developed in the Australian mallee (Kerr 1925). Outside Mediterranean regions lignotubers are rare except in a few arid savannas where they appear to be primarily involved in surviving summer drought, since aboveground parts die back annually regardless of fire (Rawitscher 1948).

Since lignotubers are not a prerequisite for resprouting after fire (resprouting is characteristic of nearly all woody dicots, Wells 1969), perhaps they are not an adaptation to fire per se, but to fire in conjunction with the Mediterranean climate. The unique combination of features found in these regions is one of shrubs growing in nutrient-deficient soils exposed to frequent fires during summer droughts. The result may be problems unique to Mediterranean-climate shrubs; they depend upon an extensive root system to obtain sufficient soil moisture and inorganic nutrients, so when the tops are removed by fire an extensive root system may not be supportable without a ready store of carbohydrates. This would be particularly so after summer fires, since resprouting is commonly postponed until the first fall rains (Sauntier and Wagle 1967, Biswell 1974, Tratz and Vogl 1977). Such an hypothesis would account for why the non-burl-forming sprouting species (group 2) favor the more mesic slopes.

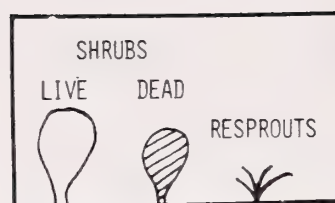
OBLIGATE-SEEDING SHRUBS

So lignotubers may not represent a specialized adaptation to fire per se, but to fire within the context of the Mediterranean climate. Another characteristic of reproductive modes in some Mediterranean floras is the high proportion of species (in genera where lignotuberous species are common) totally lacking the ability to resprout after fire. In California, for example, approximately one-third of the Ceanothus and Arctostaphylos species resprout from lignotubers after fire in addition to postfire seedling establishment. The rest of the species are incapable of resprouting and thus are obligate seeders. A similar array of genera with lignotuberous species and obligate-seeding species is found in the Australian mallee (Specht and others 1958) and the South African fynbos (Kruger 1977). Such species, which lack ability to resprout from underground parts, are rare among woody dicots (Wells 1969). That these obligate seeders are "fire-type" species as suggested by Jepson (1916) is supported by their high frequency in the chaparral, mallee, and fynbos and their absence in the Chilean matorral, a Mediterranean-climate region of low natural fire frequency (Mooney 1977b).

The adaptive significance of obligate-seeding species is not obvious. Evidence that the California obligate-seeding species were derived from lignotuberous sprouting ancestors is given by Wells (1969) and Stebbins (1974). Obligate-seeding species likely evolved on sites where high mortality of resprouters favored reallocation of energy from lignotuber to seed production. This would follow because: (1) resprouting is less useful on such sites and (2) fewer resprouts mean less competition for seedlings and thus a greater premium on seedling production. Therefore, obligate seeders are dependent upon fires which create large openings for seedlings at the expense of resprouters. This could come about if fires were sporadic and occasionally there were long periods of time between fires; there would be fewer shrubs alive, thus fewer potential resprouts, and fewer still would survive the more intense fires (fig. 5). Obligate seeders can survive long periods without fire as seeds in the soil. This scenario would be exacerbated on more xeric sites since (1) these sites would have fewer shrubs (and thus fewer resprouts) and (2) fires would tend to be more intense regardless of the age, and thus result in higher mortality of resprouters. It is of interest that obligate-seeding species favor the driest slopes and ridgetops whereas north-facing slopes, which support an abundance of vigorous resprouters, are the least favored sites. Specht (1980) describes a similar situation in the Australian mallee where in humid areas the high density of resprouters tends to suppress obligate seeding, whereas in drier habitats they survive in gaps between the more widely spaced resprouters.

PREFIRE ASPECT

25 years



100 years

POSTFIRE ASPECT



SHORT FIRE CYCLE

1. FEWER DEAD SHRUBS PRIOR TO THE FIRE
THUS, MORE POTENTIAL RESPROUTS
 2. LESS INTENSE FIRES
THUS, LOWER MORTALITY OF
SPROUTING SHRUBS
- THE RESULT IS SMALLER OPENINGS
FOR SEEDLINGS
- CONCLUSION: LOW SELECTION PRESSURE
FOR OBLIGATE-SEEDING



LONG FIRE CYCLE

1. MORE DEAD SHRUBS PRIOR TO THE FIRE
THUS, FEWER POTENTIAL RESPROUTS
 2. MORE INTENSE FIRES
THUS, HIGHER MORTALITY OF
SPROUTING SHRUBS
- THE RESULT IS LARGER OPENINGS
FOR SEEDLINGS
- CONCLUSION: HIGH SELECTION PRESSURE
FOR OBLIGATE-SEEDING

Figure 5.--Model of the relationship between successional changes in the density of live shrubs and relative abundance of postfire resprouting shrubs resulting from fires early vs. late in succession (redrawn from Keeley and Zedler 1978). See Brown (1958) for enhanced resprouting under frequent fires and Keeley and Zedler (1978) and Schlesinger and Gill (1978) for thinning (and change from contagious to random distribution) in older chaparral.

Mediterranean-Climate Deciduous Scrub

Most Mediterranean climate regions have a summer deciduous highly aromatic sub-ligneous vegetation on the drier margins of evergreen scrub. From what little is known of this vegetation (for all regions) it seems the southern California Coastal Sage Scrub is representative. This community is characterized by closely spaced shrubs 1-1½ m tall. It is best developed at lower elevations, on xeric sites, in midst of chaparral. Due to its coastal location, it is distant from lightning storms which are concentrated at higher elevations inland (Keeley 1977b). This, coupled with prevailing on-shore winds during thunderstorms, militates against a high natural fire frequency for this vegetation (Sauer 1977, Byrne and others 1977).

The longevity of these shrubs is not well known; in one instance shrubs over 40 years old were quite vigorous (Keeley, unpublished data). All species produce abundant light, wind-dispersed seeds. The extent of seed storage in soil until fire is unknown. However, no coastal sage species is known to require fire scarification to

(Mirov and Kraebel 1937, Keeley unpublished data). Also, seedlings of most coastal sage species readily establish without fire, in openings in coastal sage vegetation (personal observation), or openings in chaparral (personal observation; Patric and Hanes 1964). Postfire regeneration is poorly understood. All species, even the most suffrutescent ones, are vigorous resprouters from caudices and (in some species) root systems (Keeley unpublished data). Postfire resprouting, however, is apparently sensitive to fire intensity since these shrubs (when found in association with chaparral) are often reported as nonsprouters. Apparently most coastal sage species do not store seeds in the soil until fire. This is suggested by the recent discovery that shrub seedling establishment in the first postfire year is nil (J. Keeley unpublished data). Most shrub resprouts, however, flower the first year after fire and establish abundant seedlings the second year.

Humid Evergreen Scrub

On poor soils throughout the mild and humid coastal plain of the southeastern United States is a shrub vegetation. On sandy soils in maritime situations it forms a dense scrub whereas in bogs it is interspersed among, and often successional to, other vegetation types (Schlesinger 1978). This region is characterized by precipitation throughout the year and frequent spring and summer lightning storms. Natural fires can occur only in very dry seasons and are not always common (Webber 1935).

The vegetation is a dense tangle of broad-leaved evergreen sclerophyllous-leaved shrubs, distinctly lacking herbaceous understory. Little is known about the reproductive characteristics of these shrubs. Seeds are mostly animal dispersed with some species producing acorns, others fleshy drupes. Seedling establishment is apparently rare under mature shrubs and there is little viable seed storage or none that survives fire, since seedlings do not establish after fire (Webber 1935). Vegetative reproduction is uncommon though all species regenerate vigorously from rootstocks after fire, even in the face of repeated frequent fires. Under natural conditions, the fire frequency is low, since moisture content of the vegetation is usually high and there is no herbaceous vegetation to carry a fire. In fact, the dearth of herbs extends into a "bare zone" around the edge, preventing fires from being carried into the scrub from adjacent savannas (Webber 1935). This scrub vegetation can withstand long fire-free periods since most of the shrubs are long lived, often becoming small trees. They probably owe their existence to occasional periods with frequent fires which eliminate pines and to poor soils which slow reinvasion by the pines or sprouting hardwood trees.

Once scrub vegetation has established, it is maintained by resprouting after fire. Seed production appears to contribute little to continuation of the stand; rather, seeds are dispersed elsewhere. Once in a new area, seeds germinate, and may infrequently establish new shrubs beneath the sparse canopy of certain pine formations. Given a peculiar sequence of frequent fires (which eliminate some pines but allow resprouting shrubs to remain) coupled with infrequent fires (which allow for establishment of new shrubs), there may be slow attrition and eventual replacement of pines with scrub vegetation.

Arid (Desert) Scrub

Scrub vegetation in arid regions frequented by summer thunderstorms is common in both the temperates and tropics. Lightning fires are frequent though the spread of fire is often limited by lack of fuel. This vegetation is well developed throughout southwestern North America where it consists mostly of spiny shrubs and subshrubs. Seed production is erratic from year to year. The seed of many species requires scarification and this can come about in a variety of ways. Thus, seedling establishment can occur without a fire, though it is erratic and probably linked to precipitation patterns.

Vegetative spread is poorly developed except for layering in some species. Most shrubs can resprout from basal portions after fire, though some species are more vigorous than others (Box and others 1967). Fires are sporadic, dependent on the buildup of herbaceous fuel coupled with a summer lightning storm. Fires are commonly destructive to seedlings and small "saplings" (Cable 1972). Older shrubs, for the most part, can survive and resprout. Few seedlings establish from soil-stored seed though it is not known whether this is due to low seed storage or fire-killed seeds. Many subshrubs produce light seeds which readily blow in and establish after fire. In general, seedling establishment is not highly dependent upon fire and will occur in all species whenever there is a favorable opening.

Temperate Forest Successional Shrubs

For a short time after fire in temperate forests, there is a successional stage of shrubs. Frequency of natural fires and type of understory shrubs is quite different in western and eastern forests of North America.

WESTERN FOREST SHRUBS

Coniferous forests, subjected to dry summers interspersed with lightning storms, are occasionally eliminated by crown fires and temporarily replaced by shrub vegetation. Shrubs are 2 to 4 m tall and capable of living 50 to 100 years, but they are normally shaded out much earlier by forest regeneration. Where regeneration is slow, due to peculiarities of the site or its history, this shrub vegetation may remain for extended periods of time.

The shrub species can be conveniently divided into two groups. One, consisting of species of Ceanothus and Arctostaphylos, produces seeds that are not well adapted to widespread dispersal. Substantial seed production begins at ca. 10 years and the seeds accumulate in soil until seed coat scarification which commonly comes about from intense heat during a fire (Cronemiller 1959, Quick and Quick 1961, Gratkowski 1962, Orme and Legee 1976). These species are found at higher elevations throughout the western United States, but as a group are best developed in the Sierra Nevada. The other group of species, e.g., Prunus, Sambucus, Rosa, Rubus, Salix, and Symphoricarpos species, are characterized by production of widely dispersed seeds with no seedcoat scarification requirement. These seeds apparently do not survive fire (Lyon and Stickney 1976) though it is not known whether in the absence of fire they remain in the soil until some other disturbance. Several species of Ribes fit neither group, having widely dispersed seeds which require scarification, usually by fire (Quick 1962).

Vegetative spread by rhizomes is common in group 2 species but not group 1 species. All species, however, can resprout from underground parts after the tops are removed by fire.

Group 1 species (Ceanothus and Arctostaphylos) seem most specifically adapted to fire. Lack of widespread seed dispersal suggests that these shrubs are adapted to widespread fires, i.e., if fires cover large areas, there is low probability of reaching a site which will burn sooner than the parent site. Thus, seeds are deposited into the soil and remain dormant until the next fire. If repeat fire occurs within a few years, these species can resprout from the root crown. As the canopy species recover and shade out the shrubs, the potential for regeneration from resprouts is eliminated. However, soil-stored seeds appear to have a great longevity as evidenced by synchronous establishment of large numbers of seedlings after fire in 400-year-old forests (Gratkowski 1962, Youngberg and Wollum 1976).

Group 2 species are adapted for dispersing into localized disturbed areas but not necessarily ones due to fires, e.g., treefalls. Also, having widely dispersed seeds, they can disperse into areas disturbed after a long disturbance-free period which would

have resulted in the deterioration of the group 1 species soil-stored seed. Since establishment on a given site is highly probabilistic, being dependent upon disturbance followed by a propagule, it is likely that some seeds will arrive sooner than others. Thus, early arriving species can benefit greatly by vigorous vegetative spread, a trait common to group 2 species but not group 1.

EASTERN FOREST SHRUBS

The predominantly winter deciduous forests of the east are characterized by cold snowy winters and some precipitation throughout the year. Moisture condition of the vegetation is usually high; consequently lightning fires seldom coincide with burning conditions (Barden and Woods 1973). Therefore, natural fires are infrequent and unpredictable and, if they did not produce conditions similar to other types of disturbance, fires might be considered catastrophes rather than disasters (*sensu* Harper 1977).

The shrub species may be evergreen or deciduous. Most are shade intolerant and thus entirely early successional. Forest regeneration is rapid; consequently, shrubs may survive only 5 to 15 years. Seed production begins early in the life cycle and is frequent and abundant (Johnson and Landers 1978). Seed dispersal mechanisms are well developed in all species. Most produce brightly colored fleshy fruits attractive to a wide variety of birds and mammals, ensuring their widespread dispersal (Smith 1975, Thompson and Willson 1978). Many species have viable seed stored in soil for long periods (Olmsted and Curtis 1947, Moore and Wien 1977), whereas others do not. Seedling establishment is uncommon without disturbance. Many species require an opening in the forest canopy for germination, the cue probably being light (Marks 1974).

Most of the species, e.g., Rubus, Vaccinium, Lonicera, Rosa, Rhus, Sassafras, Crataegus, and Symphoricarpus species, are capable of aggressive vegetative reproduction by stolons or rhizomes. The majority are capable of rapid regeneration from root crowns or caudices (Ahlgren 1960) if disturbance occurs before forest canopy closure has eliminated them. In fact, dependent upon forest structure these species may persist, e.g., Reiners (1967) showed that abundance of Vaccinium in oak-pine forest is proportional to light penetration.

Natural fire frequency for this environment is probably once every 100 to 300 years. However, other sorts of disturbances (e.g., tree falls from tornadoes, cyclones, heavy snowpack, senescence) are common. Such disturbances are localized and distributed mosaic fashion. The reproductive mode of the shrubs is closely tuned to this pattern. When localized disturbance occurs, some viable seed may already be in the soil and other seeds will come in rapidly because bird dispersers (looking for other seeds) are attracted to the openings (Thompson and Willson 1978). Early arriving seedlings will spread vegetatively, attempting to preempt as much space as possible. As the opening becomes more crowded, less energy will go into vegetative growth and more into seeds (Abrahamson 1975) which are dispersed elsewhere.

Scrub Steppe

Scrub steppe vegetation occurs in regions with deep soils and severe continental climate. Annual precipitation is low, coming mostly in the form of winter snow. Since storms are concentrated in winter, lightning fires are infrequent (Komarek 1967). In North America this vegetation is known as Great Basin Sage Scrub and natural fires are considered rare (Billings 1951 cited in Beatley 1966). The vegetation is dominated by two shrubs, Artemisia tridentata and Purshia tridentata, in association with a variety of subshrubs and grasses. Artemisia and Purshia are long-lived (100 to 200 years) evergreen "soft-wooded" shrubs, variable in size (0.5 to 4 m), dependent upon the region.

Both shrubs flower and fruit consistently, Artemisia producing an abundance of tiny widely dispersed seeds (Deitschman 1974) and Purshia fewer, larger, less mobile seeds (Deitschman and others 1974). Seeds which accumulate in mature stands contribute new individuals slowly and are greatly reduced in number by fire (Mueggler 1956). Seedling establishment is vigorous in openings or adjacent grassy areas (Humphrey 1962, Sampson and Jespersen 1963) and after fire from seed dispersing in from adjacent areas (Loope and Gruell 1973).

Other than layering on certain extreme sites, these dominant shrubs have no capacity for vegetative reproduction. For the most part neither can resprout after fire; there are exceptions, however. While resprouting is rare in most populations of P. tridentata there are certain regions with vigorous resprouting populations (Blaisdell and Mueggler 1956). That this is genetically controlled is suggested by the observation that resprouting frequency increases in populations in the southern part of its range where it overlaps and hybridizes with the closely related desert resprouting shrub, Purshia glandulosa (Nord 1965). The increase in resprouting from north to south among the two species may be related to a similar gradient in increasing summer thunderstorms and natural fire frequency.

Data from Wyoming indicate that fire frequencies between 10- and 20-year intervals are sufficient to replace A. tridentata with bunchgrasses, but it readily reestablishes given an 80-year fire-free period (Houston 1973), and this time frame is supported by studies in Utah (Pickford 1932). Given a longer fire-free period than this, juniper can invade and replace sagebrush (Barney and Frischknecht 1974). This, however, requires a seed source area immediately available since rapid juniper invasion is generally restricted to ecotonal areas between the two vegetation types (Burkhardt and Tisdale 1976). Thus, long fire-free periods throughout much of the Great Basin probably would not result in juniper invasion.

Tropical Rain Forest Understory Shrubs

Scattered short-statured shrubs occur in the understory of lowland tropical forest in both the Old and New World. Precipitation is evenly distributed throughout the year so that the moisture condition of the vegetation essentially precludes natural fires (Phillips 1965). Palms are an important part of this understory vegetation. A typical example is Podococcus barteri, a common African understory palm.^{2/} Flowering and fruiting occur over many months and actual seed production may be quite small. Fruits are fleshy and likely animal dispersed. Seedling establishment is not common. Most reproduction is due to clonal spread from stolons. An individual is estimated to live for more than 100 years. It was estimated that stolon production began after about 15 years with flowering beginning after 40 years. In contrast to Podococcus is the New World tropical understory palm Cryosophilia guagara. This species establishes seedlings under the closed canopy. However, a break in the canopy is required for the seedlings to develop further and reproduce (Richards and Williamson 1975).

Summary: Shrub Communities

Mediterranean evergreen scrub vegetation represents a number of specialized adaptations to fire. The most prominent have poorly dispersed seeds, fire-stimulated germination, basal burls, or obligate-seeding shrubs. Lack of well-developed seed dispersal mechanisms in the dominant species (90 percent by cover, Bullock 1978) may stem from widespread fires. Seed germination cued to fire reflects the inhospitality of chaparral understory (low light and high predation) coupled with predictability that fire will occur before much of the canopy dies. Basal burls may represent a response to problems unique to Mediterranean shrubs; maintenance of an extensive root system when the tops have been removed but conditions are unsuitable for their

^{2/} Bullock, S. H. Demography of an undergrowth palm in Biafran rain forest. Unpublished ms.

immediate restoration. Obligate-seeding species are another unique feature of most Mediterranean regions. They may have evolved in response to an increasing number of sites on which resprouters could not succeed. The outcome would be twofold: (1) large "openings" for seedlings, thus selection for higher seed production, and (2) less chance of resprouting, thus less intense selection for maintenance of a burl; in sum, a reallocation of energy from burl to seed. This scenario is supported by evidence that California obligate-seeders arose from burl-forming ancestors. This may account for loss of the burl. Loss of sprouting per se may be due to ineffectiveness of resprouting without a burl on the more xeric sites. Thus, Mediterranean scrub represents one of the most specialized vegetations with respect to fire. These adaptations reflect high predictability of fire in the environment. However, they do not reflect the predictability of frequent fires, i.e., the vegetation as a type is degraded by too frequent fires and not obviously affected by fires as few as one per century (Keeley and Zedler 1978).

Southern California Coastal Sage Scrub is a vegetation type further removed than chaparral from natural fire sources, thus fire is more unpredictable. Postfire regeneration occurs from sprouts in some cases and from seed either in the soil or blowing in. If fires are too frequent, coastal sage is replaced with grass. Shrub seedlings can establish in openings and thus this vegetation (unlike chaparral, for example) can regenerate (albiet slowly) in the absence of fire. Its well-developed colonization capacity suggests it may have played a role in a sort of gap phase succession with oak woodland prior to increased fire frequencies (and elimination of much of the oak woodland) upon arrival of hominids in southern California (Wells 1962). Today, coastal sage species colonize chaparral areas thinned out by too frequent fires.

The coastal plain evergreen scrub of the southeastern U.S. resembles Mediterranean-climate scrub in many ways (sclerophylly, evergreenness, small leaves, sprouting, deep roots, lack of herbaceous understory, and sometimes a peripheral "bare zone"). The structural features are general adaptations to a variety of semixer environments (Axelrod 1975). However, this is where the similarities end. Coastal plain scrub differs from chaparral in that seeds are not stored locally and stimulated by fire to germinate, and there are no burl-forming or obligate-seedling shrubs. Although coastal plain scrub is not as specialized to fire as chaparral, it exhibits much greater resilience to high fire frequency.

Desert scrub vegetation can recover following occasional fires, predominantly from resprouting. Seedling establishment occurs without fire, thus many age classes are present when fire occurs resulting in the younger age classes being killed. Consequently, frequent fires may result in an unstable age structure. In the absence of fire, desert shrubs are capable of maintaining themselves. The fact that summer lightning storms occur and that desert shrubs such as Purshia glandulosa, have evolved or maintained the resprouting ability when a closely related congener, P. tridentata has not, suggests fire may have been a selective agent in this vegetation.

Temperate forest successional shrubs exhibit two strategies. One which is best developed in the more western forests is similar to the predominant chaparral shrub strategy. It involves shrubs which lack vigorous vegetative reproduction and produce poorly dispersed, long-lived, fire-stimulated seeds. The shrubs are all relatively resilient to fire, all able to resprout if fires are too frequent, and all remain dormant as seeds if fires are infrequent. Widespread fires have probably selected against dispersal mechanisms. Local seed storage in the soil results in abundant seedling establishment following fire; consequently, less is to be gained by spreading vegetatively than growing vertically. The second strategy (most highly developed in eastern forests) involves shrubs with vigorous vegetative reproduction and widely dispersed seeds lacking any seedcoat scarification requirement. Widespread seed dispersal suggests adaptation to a more localized disturbance, of which fire may be only one type.

Since disturbances other than fire result in openings for these shrubs, there has been no selection for heat-stimulated germination. Also, a seed reaching an opening first will benefit by spreading vegetatively and preempting space. All of these shrubs resprout after the tops are removed, thus frequent fires are not harmful; nor is the complete absence of fire harmful, since other disturbances are probably common enough to maintain these shrubs.

Steppe-type scrub shows little dependence upon fire except in defining the border between it and juniper woodland at the base of various mountain ranges. The dominant shrubs do not resprout and revegetation following fire requires recolonization from the outside. Thus, this vegetation is not resilient to frequent fires and can maintain itself throughout most of its range without fire.

Tropical understory shrubs probably have had no evolutionary influence from fire. Some resemble temperate forest successional shrubs in dependence upon openings and strategies for getting to them. Others are shade tolerant and not dependent upon disturbances and instead exist as understory shrubs. Vegetative spread is the dominant reproductive mode. Reduced seed production may reflect the dwindling importance of two common functions of seeds: (1) to provide a dormant stage and (2) to provide a dispersal agent.

TREE VEGETATION TYPES

A list of the major tree vegetation types considered here is given in table 5. Note that in addition to the life history responses listed in table 1, trees, unlike herbs and shrubs, have the capacity to resist fires through their tall growth form in conjunction with self-pruning and thick fire-resistant bark. In some instances, resistance to fire may be as important as (and functionally similar to?) resprouting.

Temperate Coniferous Forests

Throughout temperate regions of the world are a variety of coniferous forest types. I will focus here on a few communities and individual species from North America which represent responses from low to high fire frequency.

SEQUOIA MIXED CONIFER FOREST

Throughout the Sierra Nevada Range of California, between 1 000 and 2 000 m elevation, is a forest dominated by Pinus ponderosa, P. lambertiana, Abies concolor, and Calocedrus decurrens with scattered groves of Sequoiadendron giganteum. The climate is Mediterranean with most of moisture coming in the winter as snow and the summers subject to droughts. Summer thunderstorms are frequent and although they contribute little to the annual precipitation they provide a source of lightning fires.

Studies of tree-ring chronologies in fire-scarred trees indicate that, during the 18th and 19th centuries, widely separate areas had fire frequencies ranging from 2 to 20 years with an average interval of 5 to 10 years (Wagner 1961, Kilgore 1973). Evidence indicates that aboriginal man who occupied parts of this region for the last 1,000 years contributed substantially to this frequency of fires. Reynolds (1959) provided evidence of this for the central Sierra Nevada by demonstrating the unlikelihood that lightning fire frequency could account for fire scar frequencies in trees of this region. By comparing fire scar frequencies from different historical periods Kilgore and Taylor (1979) have also provided substantial evidence of Indian influence on past fire frequencies for the southern Sierra Nevada. Their data show an approximate five-fold decrease in fire scar formation after the elimination of the Sierran Indian culture (1870's) but before the U.S. fire suppression effort around 1900 (fig. 6). Thus, a "natural" fire frequency (natural in the sense that life history attributes evolved long before Indian occupation) for the mixed conifer forest is lower than the fire scar data indicate.

TABLE 5.--Principal tree vegetation types, estimated natural fire frequency, and a rough estimate of the minimum and maximum fire-free interval to which they are resilient

Vegetation type	Modal fire frequency	Minimum fire-free interval	Maximum fire-free interval
	- - - - - <u>Years</u> - - - - -		
Temperate coniferous forests:			
sequoia mixed coniferous forests	10-100	1-3	600
Lodgepole forest -			
Sierra Nevada	100-300	?	∞
Lodgepole forest -			
Rocky Mountains	40- 80	15	200-300
Southeastern pine savanna	20- 50	0	200
Pine barrens	10- 20	1-3	200
Chaparral conifers -			
<u>Cupressus</u>	50-100	20	200?
<u>Pinus</u>	20- 40	10	100
Pinyon-juniper woodland	100-300	100	∞
Boreal forest	20-300	?	∞
Temperate deciduous forest	100-500	25	∞
Tropical rain forest	∞	∞	∞

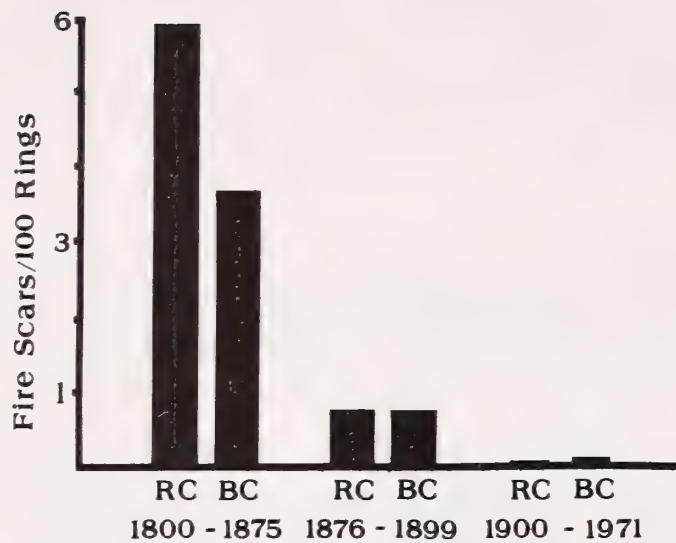


Figure 6.--Number of fire scars per 100 annual growth rings in trees from two sites in the southern Sierra Nevada, presented by historical period; (1) 1800-1875 includes Indian and lightning set fires, (2) 1876-1899 there was no Indian burning, only lightning and settler-set fires, but no fire protection, and (3) 1900-1971 fire protection. RC = Redwood, number of trees = 37; BC = Bearskin Creek, n = 183 (based on data from Kilgore and Taylor 1979).

Extrapolating from Kilgore and Taylor's data, the natural fire frequency is approximately one-fifth of that indicated by tree chronologies. A reasonable range might be 10 to 100 years with a 25- to 50-year mode. Given these bounds, the mixed conifer belt very likely evolved under a temporal mosaic of fire frequencies; e.g., periods of frequent ground fires interrupted by an occasional hiatus in fires and terminated by a severe crown fire. The rugged topography of this region would promote irregular burning patterns and further contribute to this mosaic of frequent ground fires interspersed with severe crown fires. It should be kept in mind that when John Muir stated, "In the main forest belt of California fires seldom or never sweep from tree to tree in broad all-enveloping sheets" (Muir 1938), he was reflecting the fire regime resulting from widespread Indian influence. Notwithstanding, there is evidence of occasional widespread crown fires even during this period (Burcham 1973, Reynolds 1959, Wagener 1961).

The influence of a temporal mosaic of ground fire and occasional severe crown fires is reflected in the life history attributes of the shrubs (see previous section) and trees of this region (Fowells 1965). The dominant trees are long lived, most species surviving 300 to 600 years (*P. lambertiana* to 1,000 years, *S. giganteum* to 3,000 years). Substantial seed production begins between 40 and 120 years, with *P. ponderosa* at the lower end and *P. lambertiana* and *S. giganteum* at the upper end. Annual seed production fluctuates with "good" years occurring at intervals of 3 to 9 years. Seeds are wind-dispersed and although most species have winged seeds, the bulk of the seed crop falls within 50 m of the parent tree. However, the small amount dispersed further may be significant in some instances, since seedling establishment in most of these species is dependent upon an exacting set of microsite conditions. For example, *P. ponderosa* and *S. giganteum* seedlings require highly lit, mineral-soil sites, whereas *A. concolor* establishes best in litter beneath the canopy of shrubs or trees. In all species, seed storage in soil is insignificant.

Vegetative reproduction or regeneration from sprouts is essentially unknown in these species. Resistance to fire varies widely both between species and between age classes within a species. In general, seedlings and saplings of all species are sensitive to fire, even light ground fires (Connaughton 1934, Hartesveldt and Harvey 1967). Kilgore and Taylor (1979) found that the youngest age at which fire scars were laid down was between 15 and 20 years in most species, suggesting that trees younger than this did not survive fires. Thus, for the first couple of decades of a sapling's life, survival is greatly enhanced by lack of fire.

Today, the mixed conifer forest is a patchwork mosaic of various species combinations (Kilgore 1973) which very likely reflect differing species' tolerances or optima in fire regime. For example, mature P. ponderosa are tall, thick-barked trees which self-prune and thus can withstand centuries of light to severe ground fires. Seedling establishment requires a local seed source, a relatively open site such as after a crown fire followed by a period of years without fire. Thus, occasional ground fires distributed mosaic fashion, which by chance happen to skip patches of forest for many years, would result in a patchwork of small crown fires near seed source trees. The cohort of seedlings established after such a disaster would in later years be thinned by ground fires and eventually result in a localized even-aged stand which is commonly the case for P. ponderosa (Fowells 1965). Sequoia seems to have a life history adapted to a similar scenario, i.e., ground fires which thin the understory and thus ensure the survival of some seed source trees, coupled with the occasional localized severe fire which opens the forest canopy. In general, S. giganteum seedlings establish and survive best on open sites after severe fires followed by a lack of burning (Hartesveldt and Harvey 1967).

In contrast to these two species, Abies concolor is dependent upon the existence of sites which remain fire free for extended periods. Although their thin bark and lack of self-pruning make them sensitive to ground fires, older individuals can survive light fires. Seedlings, however, do not establish well in openings, rather they do best beneath the canopy of other vegetation. Thus, mature A. concolor is able to survive on sites periodically burned with light ground fires; however, seedling establishment and development to maturity is dependent upon localized sites which remain free of fire for extended periods. Given enough time, conditions suitable for a crown fire can occur in a white fir stand replacing it with ponderosa pine. Increased establishment of A. concolor since presettlement times is well documented and it is generally agreed this is due to decreased frequency of fire. What is not generally appreciated is that, although present densities are unnaturally high due to fire protection, presettlement levels were unnaturally low due to Indian burning. This is illustrated by Kilgore and Taylor's (1979) demonstration that (1) a large surge of Abies following collapse of the Indian cultures (ca. 1870) and (2) most of the Abies establishment occurred prior to fire protection (ca. 1900).

Frequent fires represent an important component of the fire regime of the mixed conifer forest, in large part because they preserve seed source trees by "breaking up" the region and thus prevent widespread crown fires. This is critical since seeds are not stored in the soil and long-range dispersal is poorly developed. However, fires are not ubiquitous, and localized areas throughout the region remain unburned for extended periods. Species such as Abies concolor are dependent upon such sites for establishment, but eventually these localized stands are removed by severe fire and it is upon this sort of event that P. ponderosa is dependent. The other mixed-conifer trees represent adaptive solutions somewhat intermediate to these extremes. In terms of resilience all species can withstand occasional periods of frequent fires as well as extremely long fire-free periods.

LODGEPOLE FOREST--SIERRA NEVADA

At between 2 700 and 3 200 m in the Sierra Nevada is forest dominated by Pinus contorta spp. murrayana. The region is characterized by a short growing season, infrequency of droughts, sparse forests, and relative infrequency of lightning fires (Reynolds 1959). Natural fire frequency for this vegetation is apparently very low. This is suggested by results from the Natural Fire Management Zone in Sequoia and Kings Canyon National Parks. This zone includes over 200 000 ha generally above 2 600 m, in which all naturally ignited fires are allowed to burn (Parsons 1977). Over a period of 9 years less than 2 percent of the region has burned, suggesting a recurrence interval for the region of several hundred years. Even when fires do occur after a long fire-free period, fuel and moisture conditions are such as to preclude extensive crown fires.

Pinus contorta, the dominant tree of this forest, is relatively long lived, attaining ages in excess of 600 years. In most respects seed production characteristics are similar to other pines in this region, i.e., production of winged seeds more or less locally distributed establishing best on exposed mineral soil. Unlike populations of P. contorta in the Rocky Mountains, there is no tendency towards serotiny in Sierran populations. Pinus contorta differs from pine species found in more fire-prone regions in that it has relatively thin bark, self prunes poorly, and in more open stands has branches near the ground.

Thus, fires are uncommon in the lodgepole type as are adaptive characteristics for surviving fires. Seedling establishment is generally on sites exposed by tree-falls or in meadows following a change in water table.

Lodgepole Forest--Rocky Mountains

In some parts of the Rocky Mountains, Pinus contorta populations produce mostly serotinous cones (Critchfield 1957) and this is apparently genetically controlled (Lotan 1967, Teich 1970). The climate of this region is continental with some precipitation occurring during summer months (particularly accompanying lightning) so that conditions conducive to fires occur at infrequent intervals (Loope and Gruell 1973). Lodgepole pine occurs at lower elevations than in the Sierra Nevada (1 800 to 2 400 m), therefore the growing season is longer and forests more heavily stocked and summer dry periods more likely to occur. Fires are infrequent in this region, but when they occur they tend to be destructive crown fires (Komarek 1967, Muir 1938, Loope and Gruell 1973). Populations with serotinous cones reestablish even-aged populations after fire. Over extended periods without fire, more shade-tolerant spruce and fir will invade (Lotan 1976).

Thus, P. contorta under an infrequent but predictable and severe fire regime has taken on the role of a successional species. An obvious response to this role is the serotinous habitat. However, in many parts of its range, selection has adjusted (genetically) the frequency of serotiny to reflect local predictability of fire (Lotan 1967, Perry and Lotan 1979).

Southeastern Pine Savannas and Pine Barrens

The mild-humid forested regions of eastern North America have precipitation distributed throughout the year; therefore, even though spring and summer thunderstorms are common, burning conditions often are not conducive to fires. Drier summer conditions, and therefore fire frequency, increase from north to south, from mountains to coastal plain, and from poorly to well-drained soils (Doolittle 1977). Given an extended period free from disturbance, most of this region would support a forest of mixed hardwoods (Christensen, this volume). There are, however, several pine species prominent as successional species or more permanent members on edaphically severe sites, viz, poorly or excessively drained soils (Fowells 1965).

These pines have a number of common characteristics: (1) they are not long lived (100 to 200 years), (2) they are capable of substantial seed production at 15 to 20 years, (3) seeds are wind-dispersed, most within 50 to 100 m, (4) seed is not stored in soil, and (5) seedling establishment usually requires exposed mineral soil.

The loblolly-shortleaf pine community is the most widely distributed of the successional pine types. Dominants are Pinus taeda and P. echinata and in the absence of disturbance the former persists on very wet sites, the latter on drier low-nutrient sites. Mature individuals of both species can withstand light ground fires and young seedlings (and saplings in P. echinata) can resprout from the root collar after fire. Both pines invade hardwood sites recently cleared by severe crown fires. The tenure of this pine forest is closely tied to the sequence of fires to follow. Without

further disturbance, the hardwood sprouts may overtake and shade out the pines in 50 to 100 years. Light ground fires have little effect on this successional sequence, since the hardwoods resprout vigorously and the pines do not establish in their shade (Little 1973, Baden and Woods 1976). A severe ground fire or repeated light fires will thin the overstory and replace the hardwood understory with grasses resulting in pine savanna; this, however, will be a temporary type since these pines establish seedlings poorly under their own canopy and/or in the face of repeated fires.

These pines therefore require more or less localized disturbances which remove a portion of the canopy, but not all local seed source trees. Both species are resilient to periods of frequent fires since seedlings resprout and mature trees have thick fire-resistant bark. Neither species is resilient to long fire-free periods. Two other pines with a somewhat similar relationship to fire are P. elliotii and P. palustris. These species are less widespread and less invasive, best developed on azonal soils. Pinus elliotii is common in poorly drained flatwoods and on pond margins. Occasional fires allow establishment on better drained sites; however, seedlings and saplings are sensitive to light fires. Pinus palustris occupies sandy, excessively drained sites and has a life cycle closely cued to these xeric conditions. During the first 3 to 7 years (or longer, dependent upon soil-moisture conditions) energy is diverted from stem to root growth, producing a grasslike seedling above ground. After the first year of growth this grass stage is resistant to fire, having buds protected by needles and scales. For a period after stem growth begins, the seedling is somewhat sensitive to fires, because it does not resprout, but soon develops fire-resistant bark.

The greatest degree of adaptation to fire is found in two pines with more localized distributions, P. rigida and P. serotina, both more or less restricted to extreme sites; the former on poor sandy or gravelly soils, the latter on frequently waterlogged sites. These two trees differ from the previous species in that (1) they are more vigorous resprouters (at any age) both from root collar and stem, (2) they produce seeds at an early age (3 to 4 years in resprouts), and (3) they produce serotinous cones to varying degrees (being highly dependent upon fire history of the site [Little 1974]). In light of these specialized fire adaptations and the fact that both these species are resilient to frequent fires, it seems likely they evolved under a more frequent fire regime than associated congeners. This seems reasonable for P. rigida, since it occupies semixerix sites, but not for P. serotina which is generally restricted to bogs. It may be that P. serotina has not been exposed to more frequent fires than other southeastern pines but that fires were more devastating. This could come about in several ways. Growth on these waterlogged sites is commonly stunted, thus relative frequency of fire between stages, e.g., seedling to sapling, may be greater. Stunted growth, exacerbated by fire, would mean the crown would be exposed to severe burning more frequently. This might select for ability to resprout from the stem. Serotiny which is well developed may have been derived for similar reasons, i.e., not necessarily more frequent fires, but more severe fires.

CHAPARRAL CONIFERS

Mediterranean-climate scrub in North America is commonly associated with local patches of conifer forests within a chaparral matrix. Dominants include several species of Pinus and Cupressus, each of which have serotinous cones but do not resprout after fire and Pseudotsuga macrocarpa which resprouts but is without serotinous cones.

One species is Cupressus forbesii, a small tree occurring in small even-aged monotypic groves in the midst of dense chaparral in southern California and adjacent parts of Baja California. Substantial seed production does not begin until about 40 years of age, and for the most part seeds are not dispersed until fire opens the cones. The wingless seeds are very poorly dispersed and so seedlings establish more or less within the boundaries of the parent grove. Cupressus forbesii may owe its

existence to long fire-free periods. One advantage of infrequent fires is that it allows time for the parent plant to shade out invading resprouting shrubs which would have a competitive edge over cypress seedlings in the postfire environment (fig. 5). Its dependence upon infrequent fires is suggested by the late age at which seeds are produced, coupled with inability to resprout after fire and indications of impending extinction in stands burned at the present frequency of every 20 to 30 years. Zedler (1977a) has provided good evidence of this last point by showing that stands burned after 21 and 28 years have marked declines in density (table 6). Similar declines in populations subjected to the present man-induced fire frequency of 20 to 30 years have been described by Reveal (1978) for another closed-cone cypress (C. arizonica var. stephensonii).

Closed-cone pines associated with chaparral are similar in many respects to cypress, the major difference being their resilience to more frequent fires (Vogl 1973, Zedler 1977b). The fact that closed-cone pines and cypress seldom occur together and usually not even in the same locality suggests that they may have been segregated according to patterns of natural fire frequency.

Pseudostuga macrocarpa, unlike the other chaparral conifers, does not occur in pure even-aged stands. It is long lived (300 to 600 years) and generally found on mesic, less fire-prone north-facing slopes and ravines in association with Quercus chrysolepsis. Seed production does not begin early in life and seeds are not widely dispersed; however, seedlings establish under the canopy in the absence of fire (Sawyer and others 1977). When fires occur the youngest age classes are killed but the oldest can resprout from the stem (Bolton and Vogl 1969). Frequent fires in recent years have apparently eliminated populations at lower elevations, thereby reducing the range of P. macrocarpa (Gause 1966). Thus, P. macrocarpa like Cupressus spp. is not resilient after frequent fires. It is capable, like many nearby chaparral shrubs, of withstanding long fire-free periods.

TABLE 6.--Reconstruction of stand densities based on sample data and conservative extrapolations from data on stand structure and seedling mortality for Cupressus forbesii in San Diego, Calif. (from Zedler 1977a)

Year	Length of time since last fire	Cypress trees/m ²
<u>Years</u>		
<u>Bigrock Stand</u>		
(1944)	64	(~1.0)
(1945)	0.5	(>14.0)
1972	28	8.9
1976	1	0.60
<u>Smuggler's Canyon</u>		
(1944)	64	(~1.0?)
(1945)	0.5	(~1.5)
1965	21	>1.04
1966	0.5	(0.04)
1972	7	0.03
1976	1	0.02

PINYON-JUNIPER WOODLAND

Woodland dominated by a few species of Juniperus and Pinus occurs throughout western portions of North America. The climate is continental with sparse precipitation (250 to 500 mm/yr), usually as winter snow. Summers are hot and occasionally interrupted by thunderstorms; although precipitation is generally unavailable to the trees, these storms provide ignition for natural fires. Even so, natural fires are uncommon due to the infrequency of lightning coupled with the sparseness of the vegetation.

The dominant trees, J. occidentalis, J. scopularum, P. edulis, and P. quadrifolia are medium height (10 to 30 m) and relatively long lived (200 to 500 yrs). Seed production begins early (10 to 20 yrs); however, substantial seed production begins at 50 to 100 years. Juniper "berries" and (wingless) pinyon "nuts" are widely dispersed (often over 20 km) by birds, and these dispersed seeds have a better chance of establishing seedlings than locally deposited seeds (Salomonson 1978, Vander Wall and Balda 1977). Juniper seeds can remain dormant in soil for years until conditions are suitable for germination (usually high soil moisture) though pinyon seeds apparently must germinate the first year (Johnsen 1959, Vander Wall and Balda 1977). Seedling establishment is dependent upon chance dispersal to a favorable site (usually the protective cover of a low shrub) and ample rainfall. None of the trees have the capacity for vegetative reproduction or regeneration from resprouts, and resistance to fires is poorly developed (viz, thin bark and low branches). When fires occur in pinyon-juniper woodland, the initial effect is to eliminate the younger age classes. Continued burning will eventually replace woodland with sagebrush because the shrubs can colonize faster than the trees can reestablish.

BOREAL FOREST

At high latitudes in the Northern Hemisphere, a predominantly coniferous forest exists under a severe continental climate. The growing season is short with precipitation distributed throughout the year. Although thunderstorms are common, burning conditions are usually poor. Fires are most frequent on drier sites, but occasional droughts make widespread areas susceptible. Fires are dependent on dry periods; therefore, in the southern part of the region, fires on some sites may occur every 50 to 150 years (Heinselman 1973), whereas further north the highest frequencies may be one every 100 to 300 years (Viereck 1973), and one every 1,000 years at higher elevations (Wein and Moore 1977). The localized distribution of burning conditions coupled with the stochastic pattern of ignitions produces a mosaic of different habitats (Heinselman, this volume). Perhaps as a result, a diversity of life histories is represented by the dominants.

Pinus banksiana occurs on the driest sites (and thus most frequently burned sites) and has the greatest resilience to frequent fires. In many respects it resembles more southern pine barren congeners; in particular, it has serotinous cones. It probably is not subject to fires as frequent as, for example, P. rigida, and this may account for its lack of resprouting ability.

Populus tremuloides is an aggressive pioneer into burned areas and once established will spread by underground rhizomes and a proliferation of suckers (Viereck 1973). Repeated fires stimulate sucker growth and clones can withstand fires at intervals as short as 3 years (Fowells 1965). Substantial seed production begins after 30 to 40 years. Seeds are very light and, buoyed by long silk hairs, widely dispersed. Dispersal begins in late spring and seedling establishment is dependent upon immediate occupation of a suitable site, specifically a disturbance. Thus they capitalize on a localized burning pattern. Resilience to infrequent fires is low; areas unburned for 80 years may deteriorate from disease or invasion by shade-tolerant species (Loope and Gruell 1973).

Whereas these two species are closely dependent upon fire, two other boreal forest species, Picea glauca and P. mariana, although commonly increasing after fire, are able to persist in its absence. Picea glauca invades disturbed sites by seeds which are wind dispersed. This may be erratic, since good seed crops are sporadic (Viereck 1973), and seed is not stored in the soil (Johnson 1975). The random coupling of disturbance and good seed years probably accounts for the temporally disjunct episodes of regeneration in many areas (Payette 1976). It thrives on lowland sites; thus disturbances resulting from flooding probably create more reliable sites for establishment (Rowe 1970). Picea mariana establishes well after fire because of semi-serotinous cones, and frequently stands are even aged, dating back to the last fire (Zoltai 1975). However, it is not dependent upon fire. Some seed is dispersed every year, more in warm years or when openings in the canopy expose older cones to direct sunlight (Fowells 1965). Also, vegetative reproduction by layering is common in older trees, thus some stands can perpetuate themselves without disturbance (Zoltai 1975).

Abies balsamea requires areas free of disturbance for long periods of time, thus balsam fir is restricted to moister sites. Once established it can regenerate under its own canopy indefinitely in the absence of disturbance (Fowells 1965). Increased frequency of man-caused fires in the last 100 years has drastically reduced A. balsamea in some regions (Janke and others 1978).

Temperate Deciduous Forest

Temperate latitudes in both hemispheres support belts of deciduous hardwood forests, e.g., North America's Eastern Deciduous Forest. The climate is one of cold winters and warm-humid summers, with precipitation year round. Thunderstorms are common in spring and summer, but because of the moist-humid conditions natural fires are uncommon (Barden and Woods, 1973). When fires occur it is due to widespread droughts and consequently fires are frequently large (MacLean and Wein 1977). It has been estimated from laminated sediments in Green Leaf Lake, Ontario, that since 770 A.D. fires have occurred at least once every 80 years in the vicinity (Cwynar 1978), though much of this may have been due to extensive burning by Indians (Frissell 1973). It is estimated from the total acreage burned by natural fires since settlement of a tract in Maine, that the recurrence interval of burning for that forest is 800 to 2,000 years (Lorimer 1977). Windfalls (from one to hundreds of trees) are perhaps selectively a more important disturbance in these forests: they are more localized than fires but occur much more frequently (Stearns 1949). Therefore, the Eastern Deciduous Forest emerges as a relatively stable forest in a matrix of frequent local disturbances and occasional widespread fires.

Such a selective environment is reflected in the life histories of the trees. This is illustrated by the size distribution of a forest studied by Goff and Zedler (1968), shown in figure 7. The diagram suggests that the area was disturbed some time in the past and first invaded by Pinus strobus and later by Acer rubrum. Both species have well-developed colonizing features, i.e., they produce many seeds which are light and widely dispersed by wind and have rapid germination and growth once they reach openings. Perhaps a cost of this strategy is less competitive capacity once the more shade-tolerant species (e.g., Acer saccharum, Tsuga canadensis) close in the canopy. This is evidenced by lack of new individuals added to the larger size classes of A. rubrum and P. strobilus. Consequently, seeds of these species must land in another opening to complete their life cycle. For these early successional species (since disturbances are small and haphazardly distributed in time and space), evolution has selected for a variety of ways of enhancing the chances of seedlings establishing in openings and also of being some of the first to establish. For example, figure 7 shows that although A. rubrum does not mature under the forest canopy, it does establish seedlings. These can survive, albeit stunted, for various periods of time. In the event of an opening above them, they exhibit "release" (rapid growth) and thus have a headstart on species like P. strobilus which must disperse in.

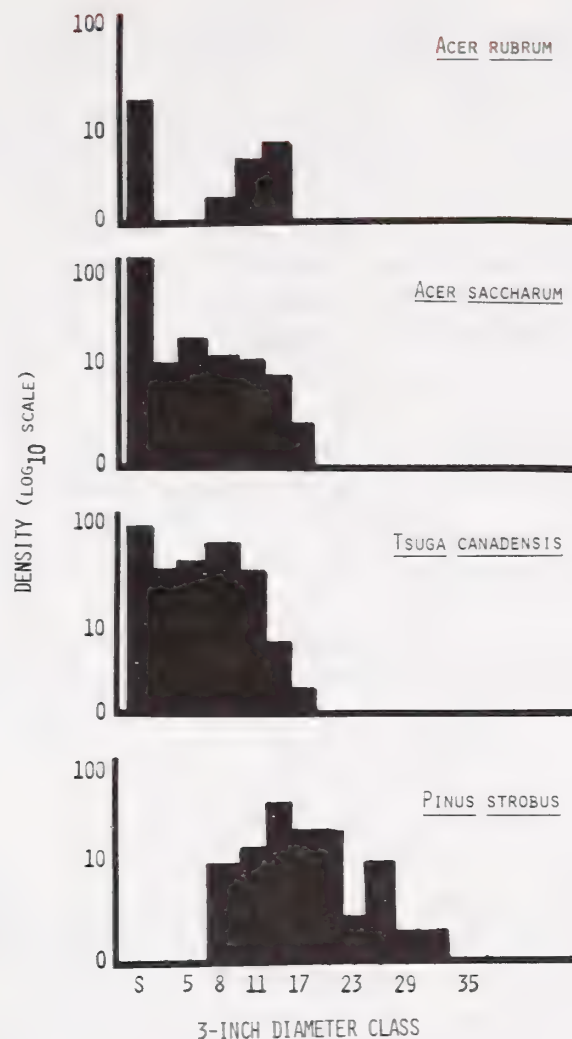


Figure 7.--Density distribution in relation to diameter for a Wisconsin forest (redrawn from Goff and Zedler 1968). S = seedlings.

There are other colonizing strategies found in early successional trees. *Prunus pennsylvanica* produces an abundance of fleshy drupes which attract many bird species and are widely dispersed (Smith 1975). By being bird-dispersed, the chances of having the seed deposited in an opening are increased (over wind-dispersed seed) since birds are biased towards sunny areas (Thompson and Willson 1978). In the event the seed is not excreted in an opening, it is protected by a hard endocarp and can remain dormant in the soil for many years until disturbance occurs (Marks 1974). Several other ways of ensuring a seed source is available are seen in species of *Cornus* which mature and reproduce in the understory of better lit portions of the forest or in *A. rubrum* which can persist a long time in the forest canopy. Regardless of the length of time they persist, the clumped distribution of individuals (relatable to previous disturbances) is sometimes still observable many years after disturbances (Williamson 1975). Most early successional species also exhibit little periodicity in annual seed production (Marks 1974, Wells 1976), reflecting the importance for a rapid invasive capacity; a several-year delay between disturbance and a good seed year could spell failure for a fugitive species.

A few early successional species will fill openings laterally by vegetative reproduction; however, most species do not, and instead attempt to reach the canopy. Essentially all species are capable of resprouting from root collar after the tops have been damaged, and openings are commonly filled by resprouts in both successional and climax species.

Climax species are those which are shade tolerant and therefore capable of establishing beneath their own canopy and replacing themselves. They produce larger seeds which probably are not dispersed as widely as those of early successional species. Larger seeds provide a larger food source for the seedling, a necessity for establishing under the canopy. Lower light levels on the forest floor mean slower growth rates, therefore longer disturbance-free periods are required to establish. Fleshy fruits are uncommon perhaps because the large seed size would require a fruit too large to be effectively dispersed by birds and rapid arrival at openings is of little value due to the slow growth rates. For this reason, too, extreme periodicity in annual seed production (common in climax trees) is of little disadvantage. On the contrary, since these species do not produce an expendable exocarp (as in a drupe) animals attracted to a seed crop destroy much of it, thus mast years may serve an antiherbivore function (e.g., Janzen 1976). Another characteristic of the reproductive strategy of "climax" trees is a lack of long-lived soil-stored seed (Olmstead and Curtis 1947). In most respects "climax" species are only quantitatively different from "successional" species since they commonly require subtle disturbances in order to establish or be "released" and enter the canopy (Forcier 1975, VanKat and others 1975, Brewer and Merritt 1978, Harcombe and Marks 1978). The ubiquity of some disturbance-dependence is reflected in Wells' (1976) finding that although some plant families have specialized (ecomorphologically) at the pioneering extreme of the seral gradient, none have a consistent suite of traits specialized on the climax end.

Tropical Rain Forest

At low latitudes in the Old and New Worlds are forests of broad-leafed evergreen trees existing under a wet-humid tropical climate. Natural fires are essentially nonexistent; however, as in temperate forests, disturbances such as windfalls can be common and when resulting from cyclones or hurricanes they can cause widespread damage (Longman and Janik 1974). Therefore, tropical rain forests, like certain temperate forests, exist as a relatively stable vegetation in a matrix of localized disturbances (Hartshorn 1978). Therefore, one would predict similar reproductive strategies in the dominants. Although much more is known about the reproductive cycles of temperate species, it seems that tropical trees represent a similar seral spectrum of strategies keyed to colonization of disturbed sites. At the pioneering end the Bombacaceae represents a tropical analogue to the temperate Salicaceae in its suite of ecomorphological traits, e.g., light, widely dispersed seeds, rapid growth rate, shade intolerance, and short lifespan (Wells 1976). Like their temperate counterparts, tropical pioneering trees represent a variety of families and adaptive specializations. Also, as in temperate forests, one can detect patches of regeneration which are perhaps related to previous disturbances (Richards and Williamson 1975). In response to disturbance one of the important aspects of the reproductive cycle of tropical trees is their capacity to resprout. In fact, Webb and others (1972) found that 12 years after disturbance, "suckers" were of much greater importance than seedlings. As in temperate forests, the one reproductive strategy not found in climax species is production of long-lived soil-stored seed (Webb and others 1972).

Summary: Tree Communities

The Sierra Nevada Mixed Conifer Forest has had a long history of relatively frequent ground fires. The rugged topography of this region promotes irregular burning patterns. Once an area is "missed" the burned periphery might act as a firebreak for many years. As a consequence, localized areas may be free of fire for long periods and then the site of a severe crown fire. Thus, the landscape would be a mosaic of different fire frequency patches. Species such as Pinus ponderosa have adapted to more frequently burned patches by being able to resist fires through development of thick bark, self-pruning, etc. Those species such as Abies concolor which have adapted to less frequently burned patches are less fire-resistant but have

shade-tolerant seedlings which can establish in areas free of disturbance. All species are dependent upon maintaining seed-trees throughout the region since seeds are not widely dispersed or stored in the soil. Frequent fires accomplish this by burning around fire-resistant trees and making them "immune" to localized severe fires and by haphazardly missing patches which preserve shade-tolerant fire-sensitive trees. The localized fire-free patches not only provide a haven for fire-sensitive species, but also, because they will eventually be hit by severe fire, will produce optimum conditions for establishing seedlings of shade-intolerant fire-resistant species. Since the more mesic north-facing slopes are likely to remain fire free longer and the dry south-facing slopes burn more frequently. It is not surprising A. concolor is better adapted to the former and P. ponderosa to the latter slope face.

Pinus contorta would not survive the mixed conifer forest burning regime. It is not highly resistant to fire (thin bark, poor self-pruning) and, like most pines, has shade-intolerant seedlings. However, it can adapt to infrequent light fires or periodic severe fires by a (genetically) simple change in behavior.

Several eastern pine species are unique among North American species of the genus in their capacity to resprout; a trait generally lacking in conifers. This may be due to more frequent fires though data to substantiate this is inadequate. Since these pines are on more extreme sites, slower growth rates may mean fires "seem" more frequent to the plant, i.e., a plant on a good site might go from seed to adult without a fire, whereas on an extreme site it might be exposed to several fires between seed and adult stage, even though the absolute fire frequency was the same. The more stunted growth would also place the trees in greater danger of destruction by fires. It is interesting that fire-type serotinous conifers in California are commonly found on edaphically extreme sites also (Raven and Axelrod 1978).

Among chaparral conifers are serotinous species of pine able to withstand frequent fires. Lack of sprouting capacity suggests fires have not been as frequent as in eastern pine barrens. Closed-cone cypress in chaparral suggests natural fires are less frequent than the present fire frequency. They would likely do well with fires every hundred years though they are ultimately dependent upon fire. Pseudotsuga macrocarpa has, like certain cypress species, not fared well under the current 20- to 30-year fire cycle. This is of interest since it resprouts from epicormic buds, a trait which, in light of its wide absence in conifers, was likely selected for by fire. Thus, P. macrocarpa is an example of a species able to survive occasional frequent fires because of a specific "fire-type" adaptation but the species is perhaps most favored by infrequent fires.

Pinyon-juniper conifers are unable to survive fire. They resist fire poorly, do not resprout, and do not store seeds on the plant or in the soil. In event of fire, few if any seed-source trees remain. They are capable, though, of long-distance seed dispersal by birds, a trait unknown in most North American conifers. This may be a response to very infrequent but large-scale fires. Another possibility, however, is that bird dispersal could be the only dispersal option available for the following reasons: Soil moisture is considered the most limiting factor in seedling establishment in these species, and there is circumstantial evidence that seedling establishment, in water limiting environments, is enhanced by larger seeds (Baker 1972). Also, large seeds are poorly dispersed by wind (the prevalent coniferous mode); therefore, animal dispersal could be selected for.

In the boreal forest, frequency of fires is closely linked to substrate. The driest sites support species like Pinus banksiana which resembles many other serotinous pine species. On wetter sites are species such as Picea glauca which can survive well without fire though the chance occurrence of a good seed year and local fire may favor it on burns. Picea mariana is capable of going either way; semiserotinous cones for occasional fires or layering in the absence of fire.

CONCLUSIONS

An understanding of the evolutionary role of fire in ecosystem development requires knowledge of life history characteristics. Since strategies are under genetic control, having been shaped evolutionarily, their only imperative is continuance. To understand the evolutionary role of fire frequency we need to know how it affects species' ability to remain in that environment. The following conclusions are offered in this light.

1. Since natural fires are randomly distributed in space and time, often a more important focal point than response to the modal fire frequency will be species resilience to the range in fire frequencies encountered. Failure to appreciate species-specific differences in resilience in managing natural ecosystems can spell extinction for some species. For example, it is generally accepted by managers that the chaparral ecosystem is resilient to fire every 15 to 20 years. However, it is apparent that Cupressus forbesii and C. stephensonii are in danger of extinction under this more frequent manmade fire regime.

2. Life history attributes specifically selected for by fire do not imply resilience to frequent fires and vice versa. Annual grassland species are resilient to annual fires. They are not specifically adapted to fire and do well under other annual disturbances. Fire-annual flora species have a life cycle entirely keyed to fire; however, fires at less than 10-year intervals will eliminate most of these species.

3. A component of the fire regime, important to the evolution of reproductive strategies, is the burning pattern, i.e., patchy vs. extensive. Of the four components of the fire regime, season, intensity, frequency, and pattern, the last two exert the greatest selective force, since season is relatively constant across natural systems (generally the driest season) and intensity is a function of frequency (it is largely dependent upon fuel buildup in the fire-free interval). Fire frequency relates to the predictability of fire in time and pattern relates to the predictability of fire in space.

4. There is commonly a whole suite of characteristics associated with a particular pattern of fire predictability. For example, consider the following cases of shrub reproductive strategies in response to different fire regimes.

(a) Frequent fires distributed mosaic fashion (fire is predictable in time but not space): such an environment would select for widely dispersed seeds (to "find" the disturbances), commonly without any imposed dormancy, and with vegetative reproduction (to capitalize on the probability of being one of the first there).

(b) Frequent fires burning extensive areas (fire is predictable in time and space): selection would be for locally dispersed seeds (fire will come to them), which are long lived and require fire stimulation for germination and lacking vegetative reproduction (since germination is locally synchronous).

5. "Other" environmental factors may have a similar selective effect to that of fire. For example, tree falls in many forests are more important than fire, but since they produce a similar type of disturbance, i.e., predictable in time but not in space, the reproductive strategies are similar to those described in 4a.

6. Some strategies are successful across all growth forms. For example, consider the suite of characteristics for an environment in which fire is predictable in time but not space (4a above). One can find examples of this strategy in herbs (Epilobium angustifolium, Pteridium aquilinum), shrubs (Rubus sp., Symphoricarpos sp.), and trees (Populus tremuloides, Salix sp.).

7. In some instances, strategies may be greatly influenced by growth form. For example, both perennial grasslands and chaparral are subjected to fires which are highly predictable in both time and space, yet chaparral shrubs store seed in the soil and perennial grasses do not. However, these grasses can recover from fire and flower and set seed within a few months, an option not available to shrubs. Functionally, such a response may be as fruitful as many years of seed production in a shrub, since it has been shown in at least one study that over 70 years of seed production by a chaparral shrub may result in fewer seeds stored in the soil than can be produced during a single "good" year (Keeley 1977a).

8. Resistance to fire is an attribute unique to trees, and commonly developed through the production of thick bark and self-pruning. Such resistance is required of species to survive frequent fires. As fire frequency decreases, fuel buildup increases, and the resultant fire, because of its intensity, makes resistance a nonviable option. Under very infrequent fires, there is also little selection for resistance to fire.

9. Resprouting after fire is one way an individual in the population can insure a continuance of its genes. It is such a widespread response that it is simpler to list the instances in which it is not found. One example is annual plants, another is obligate-seeding chaparral shrubs. While annual plants in some instances have evolutionarily deserted the perennial condition because of the unlikelihood of surviving a particular season, obligate seeders may have deserted the resprouting mode because of decreasing likelihood of surviving fire. Resprouting in woody dicots is a widespread, apparently conservative trait, which likely evolved many times in response to a variety of conditions; e.g., it allows for rapid recovery after frosts (Mooney 1977a), intense grazing (Sampson and Jespersen 1958), or damage from windfalls (Fowells 1965). Other than the specific instance of obligate-seeding Mediterranean shrubs, the only other common instances of nonsprouting woody dicots are ones which have a predominantly herbaceous ancestry and are currently in a more-or-less fire-free environment, e.g., *Artemisia tridentata*. In general, to argue that the presence of resprouting capacity in a woody dicot reflects the selective influence of fire is unwarranted. For example, it has been argued that the Hawaiian flora has had a long evolutionary relationship with fire because species resprout when tops are damaged. However, resprouting capacity is ubiquitous among tropical rain forest woody dicots, most of which have had no evolutionary association with fire. Gymnosperms are a different case. Resprouting is uncommon in conifers except where directly attributable to fire.

10. r- and K-selection could be interpreted to predict that growth forms should be favored in an array--herbs:shrubs:trees, relative to decreasing fire frequency. This is true when species must complete a zygote-to-zygote life cycle within the fire-free interval. It is potentially untrue whenever there is the possibility of resistance to fire or regeneration afterwards. Thus, other components of the fire regime, such as fire intensity, need to be considered.

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PREDICTING SUCCESSIONAL CHANGE

Ian R. Noble

Research Fellow
Australian National University
Canberra City, Australia

ABSTRACT

Time has dealt unkindly with generalizations about successional processes and the view nowadays tends to be that there is no grand underlying scheme behind the many and unravelled successional sequences that are observed. A number of authors have pointed out that succession seems to be accompanied by a shift from opportunistic, r-selected species early in a successional sequence to equilibrium, K-selected species later. Other authors have described a limited set of generalized successional pathways which include the classical, Clementsian, unidirectional succession as simply one case out of several. Another approach attempts to derive successional pathways from a small group of plant attributes vital to the role a species plays in vegetation replacement sequences in recurrently disturbed environments. The effects of competition and predation on the plant attributes and the selective pressures on strategies are discussed. The assumed, predominant role of competition is questioned, especially in frequently disturbed environments, and the importance of the regeneration niche is emphasized.

KEYWORDS: succession, fire, plant attributes, regeneration niche, r and K selection

INTRODUCTION

Succession is the time dependent integration of all ecological processes at a site. As such, a description of the successional sequences observed at a site incorporates the specific effects of competition and predation. Although dissatisfaction with the classical description of succession derived from Clements (1916, 1936) has existed for a long time (Gleason 1926, Cooper 1926), it is only recently that alternative descriptions of vegetation replacement sequences (plant succession) have been proposed. This paper reviews some of the alternative descriptions before discussing the selective role of competition and predation in more detail. This review emphasizes ecological succession as seen in terrestrial, higher plant communities and deals with secondary successions (Clements 1916) and, in particular, such successions in recurrently disturbed environments.

SUCCESSION AS A COMMUNITY PROCESS

Whittaker and Levin (1977) have warned that time has tended to deal unkindly with generalizations about succession since the generalities, under further observation, become confused into increasing numbers of exceptions and complications. In fact they suggest that there may be no underlying master plan (or Grand Underlying Scheme - GUS - as I prefer it) which permits the interpretation of communities, including their succession, through a limited number of strongly linked and widely significant relationships.

Nevertheless many people have sought a grand underlying scheme. Clements (1916, 1936) saw the ecosystem as a form of ontogeny. Despite Gleason's (1926) challenge to these ideas, and his emphasis on the individualism of species, a search for general community properties has dominated much recent successional thinking. Much discussion of succession has been based on the assumption that succession is a community property. This had led to emphasis of community properties such as species diversity, information content (Margalef 1963, 1968), and other gross community parameters. For example, Odum (1969) listed 24 trends to be expected in ecosystem development. The experimental and observational evidence for these trends has been questioned (Drury and Nisbet 1973, Colinvaux 1973), and Peters (1976) has pointed out that many of these trends are tautological and arise from Odum's definition (axioms) of succession or other commonly held biological principles which are effectively regarded as axiomatic. Although tautologies have a useful role in science in classifying information, they must not be confused with predictive and therefore testable hypotheses.

SPECIES' STRATEGIES

Opportunist-Equilibrium Strategy

Recently there has been an emphasis on the evolutionary strategies of the individual species and several authors have converged on an explanation of succession in terms of a displacement of opportunistic-generalist, r-strategy species by equilibrium-specialist, K-strategy species (Loucks 1970, Drury and Nisbet 1973, Colinvaux 1973, Pickett 1976). Essentially this argument states that there are opportunist species which are adapted to dispersing and colonizing unoccupied sites. These species are eventually displaced by equilibrium species which are slower growing and direct more of their resources into the exploitation of the site and less into the production of dispersal units.

Pickett (1976) has attempted to place this description of succession in an evolutionary context. He saw the amelioration of environmental extremes as a major trend in succession, and thus succession is a temporal gradient of decreasing physical stress. Drury and Nisbet (1973) also described the apparent correlation between successional trends from pioneer to more stable communities and environmental gradients from high stress to low stress situations. Pickett saw competition leading to species becoming adapted to portions of the succession/stress gradient. However, Pickett qualified this argument by admitting that the effects of competition may be masked by a meshing of life cycles, perhaps originating from competition in the past, and saw a trend in life cycles from simple, early in succession, to more complex later. The effects of other plant interactions such as allelopathy and nitrogen fixation, as well as herbivore-predator effects were recognized as important.

Pickett also argued that a gradient in genetic recombination is associated with the successional/stress gradient. Early successional species, like species adapted to high stress and unstable environments, have reduced genetic recombination (Stebbins 1958), while the equilibrium species show increased recombination and therefore produce offspring which are able to meet the slow directional change in environment. In this view, succession is a replacement of species along a temporal gradient of decreasing opportunism which is ultimately due to the interaction of different evolutionary strategies.

The opportunistic-equilibrium species description of succession is a useful contribution to ecological theory, but certain aspects of the argument need to be examined critically. For example, any relationship between successional development and the amelioration of environmental stress very much depends on the definition of environmental stress. I think that stress is a property which must be defined in terms of a particular species (or population of a species) and therefore I cannot agree that an open site following a fire is necessarily more stressful to some species than the dense litter and shade of closed forest. The description of succession in terms of opportunist and equilibrium species is not dependent on the assumption that there is an equivalence between successional change and increasing environmental stress (for example, see the description of Colinvaux 1973) and is probably an unnecessary confusion.

Similarly, discussions of the meshing of life cycles (Pickett 1976) and of trends from simple to more complex life cycles (Pickett 1976, Odum 1969) depend on suitable definitions of what constitutes complexity in a life cycle, and are probably best omitted from description of the basic processes involved in succession.

The main contribution of the opportunist-equilibrium species description is to shift the emphasis away from community properties and towards the properties of individual species. This allows a more realistic discussion of the evolutionary trends and adaptive strategies which may be important in successional sequences.

Competitive, Stress-Tolerant, and Ruderal Strategies

Grime (1974, 1977) has extended the opportunist-equilibrium argument by describing three primary strategies of plants which are related to their ability to withstand competition, stress, and disturbance. These three primary strategies arise from the interaction between the amount of stress and disturbance which is experienced at a site. In sites with low stress and infrequent or mild disturbances, a competitive strategy is most advantageous. Sites with low stress but high disturbance are associated with ruderal strategies, and sites with high stress but low disturbance with strategies of stress tolerance. High stress and high disturbance prevent the establishment of vegetation. It must be noted that Grime includes in his definition of stress any factors which reduce dry-matter production and therefore includes shading and reduction of the availability of mineral nutrients following their accumulation into plant biomass as stress rather than competition (see Chapin and van Cleve, this volume). He therefore sees succession as usually leading to a more stressful situation, rather than the amelioration envisaged by Pickett (1976).

Grime (1977) argued that competition is associated with a distinct evolutionary strategy leading to genetic attributes which maximize the capture of resources and facilitate exclusive occupation of fertile, relatively undisturbed environments (C-selection). Stress leads to adaptations for endurance of conditions of limited productivity (S-selection). These adaptations include slow growth rate and nutrient turnover, coupled with mechanisms which allow opportunistic exploitation of temporary favorable conditions. Recurrent and severe disturbance leads to adaptations which include short life cycles and rapid growth rates with a large portion of the production being directed to reproductive or persistence mechanisms (R-selection).

Grime (1977) sees ruderal strategies as corresponding to the r-selection of MacArthur and Wilson (1967), stress-tolerant strategies as corresponding to K-selection, and highly competitive species as being intermediate.

Since most sites are subject to intermediate levels of stress and disturbance, most plant species will reflect this by showing strategies incorporating components of each of the three primary strategies. Grime (1974) used a triangular model (fig. 1) to describe this, and attempted to map the approximate distribution of selected life forms on this model. Succession is seen as the replacement of species with an essentially ruderal strategy by species with increasing stress tolerance. As the productivity of the site increases, so the trajectory of the succession moves towards the competitive strategy (fig. 1c).

REPLACEMENT SEQUENCES

A second stream of successional theory has developed along with the species' strategy approach. This stream has placed more emphasis on the types of successional replacement sequences which are observed. Questions that assume more importance are: Is succession unidirectional, or can succession show multiple pathways? Or do species act to facilitate or inhibit the establishment of other species? This approach has often been directed towards the application of successional concepts to ecosystem management.

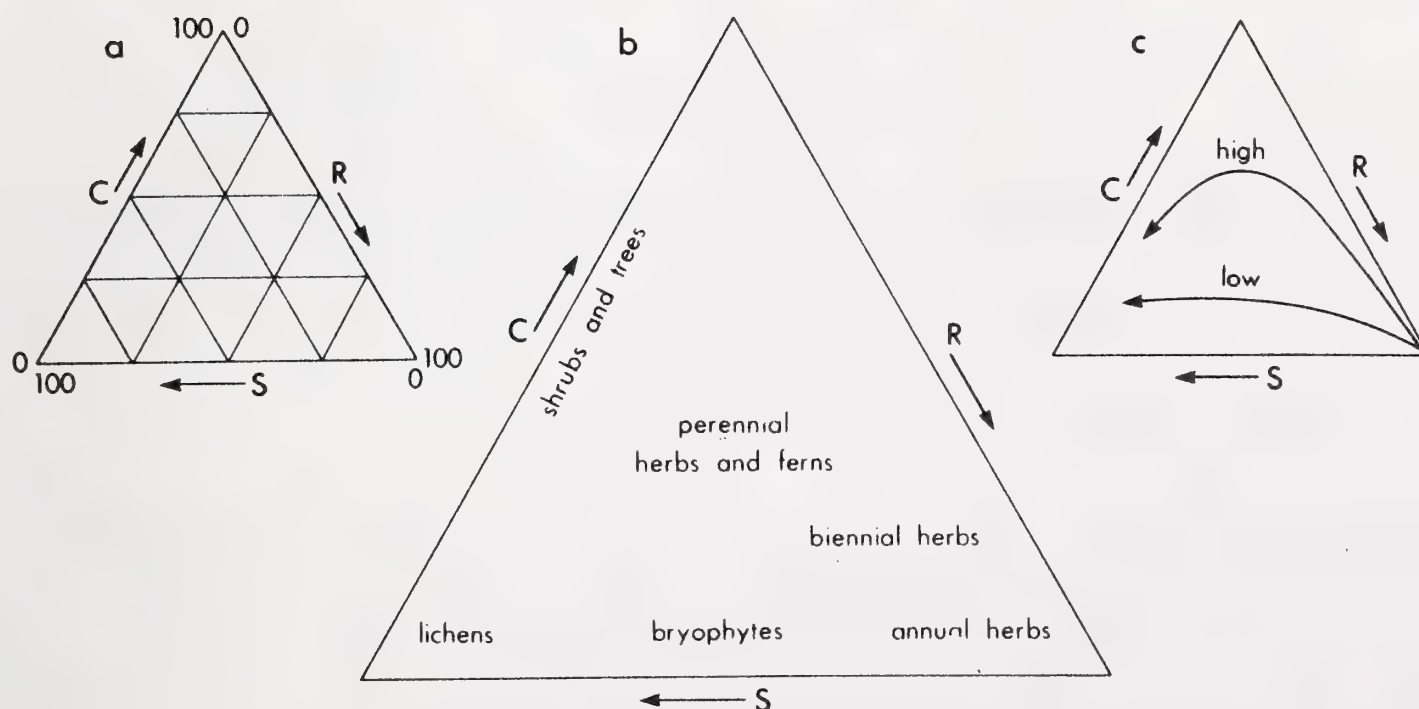


Figure 1.--Triangular model of Grime (1977). 1a - The three primary strategies, competitive (C), stress tolerant (S), and ruderal (R), are each shown on an axis. 1b - The approximate distribution of selected life forms and taxa in relation to the three primary strategies. 1c - The course of successional change in high and low productivity environments.

Classical (Clementsian) succession theory had a strong element of "altruism" incorporated in it. For example, Odum (1971) says that "species replacement in a sere occurs because populations tend to modify the physical environment, making conditions favorable for other populations." Egler (1954) questioned whether this is the fundamental process in determining vegetation replacement sequences, and concluded that in many situations the "initial floristic composition" following a disturbance is a major determinant of subsequent shifts in dominance. He emphasized that occupancy is an important factor restricting the subsequent entry of other species. Drury and Nisbet (1973) have reviewed the evidence concerning species replacement and list many examples of established species inhibiting the introduction of other, supposedly later successional species, and of the establishment of species not being dependent on the presence of their supposed precursors in a successional sequence. Connell and Slatyer (1977) have suggested that the altruistic case is only one of three possible types of interactions between species and their precursors.

Several authors have described successional pathways in addition to the simple "relay floristic" sequence described by Clements (1916). These alternative pathways (fig. 2) summarize the sequence of dominant species in a succession following a disturbance, or in a succession affected by a series of disturbances. Incorporation of disturbance into a successional sequence is an important addition to succession theory. Traditionally disturbances, such as fire, were seen as externally induced aberrations which cause regressions in an otherwise progressive successional sequence. However, in many ecosystems recurrent disturbances are a normal part of the environment and they often play a major role in shaping the composition and structure of the community.

Successional Pathways

Three distinct descriptions of succession in terms of alternative pathways appeared at about the same time. Since the scheme of Connell and Slatyer (1977) was the only one which set out to formally discuss alternative pathways, I will summarize it first. Connell and Slatyer proposed that most successional sequences involve one of three main types of pathway. The first, "facilitation pathway," is essentially the classical relay floristic pathway, in which the presence of early occupants facilitates the entry of successive suites of species. The second, "tolerance pathway," describes the situation in which later species are successful whether or not early species have preceded them; they can become established and grow to maturity in the presence of other species because they can grow at lower levels of resources. The third, "inhibition pathway," describes the situation in which later species cannot grow to maturity in the presence of earlier ones. Unless they become established along with the early occupants, their entry may be inhibited for a long period, thereby leading to dominance by species not normally regarded as late successional species.

In all models the earlier species cannot invade and grow once the site is fully occupied by their own or later species. The three models differ in the way in which later species establish once their propagules arrive at a site. The later species are either facilitated, unaffected, or inhibited by the presence of earlier species. The models also differ in the causes of death of the early species. In the facilitation and tolerance pathways the early species are often killed as a result of competition with later species; whereas in the inhibition model, the early species are killed by senescence, physical extremes, natural enemies, or local disturbances and are gradually displaced by later successional species.

Connell and Slatyer (1977) reviewed the evidence in support of the three models and found few examples in which a clear distinction between one or other of the models existed. Although observational evidence sometimes seems to support a particular model, few experimental tests have been done. They concluded that the facilitation pathway was probably common in many situations in which essentially a primary succession occurred, as for example in soil buildup on glacial moraines (Crocker and Major 1955, Lawrence and others 1967, Reiners and others 1971) or in dune stabilization (Cowles 1899, Olson 1958).

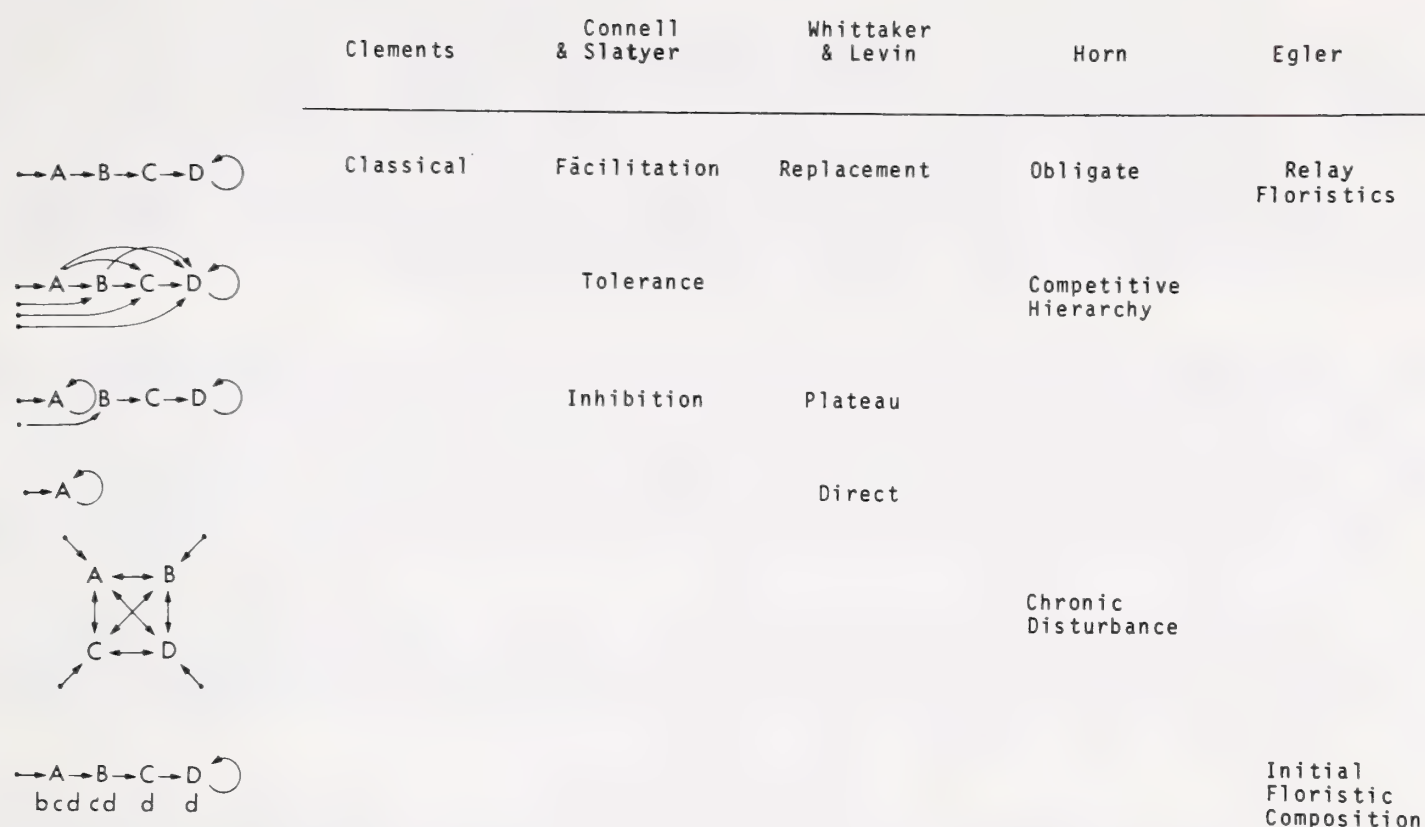


Figure 2.--Successional replacement sequences as proposed by various authors. The letters represent hypothetical dominant species; upper case indicating dominance, and the lower case subdominance. The arrows marked with a dot show alternative starting points for the replacement sequence after a disturbance.

There are many examples which show that later species do not require the presence of earlier species for their establishment, but few examples demonstrate clearly whether the "tolerance" or "inhibition" pathway applies. In most cases where there is sufficient evidence, the "inhibition" pathway seems to be supported. For example, Keever (1950) and Parenti and Rice (1969) have shown experimentally that early-colonizing plants reduce the rates of germination and growth of species arriving later, while Niering and Egler (1955) and Niering and Goodwin (1974) showed that a closed canopy of shrubs can prevent invasion by trees for several decades. The important point of the Connell and Slatyer models is that they do suggest experimentally testable hypotheses, and the conclusions from these tests are of direct practical value in ecosystem management or prediction.

Whittaker and Levin (1977) described four types of succession, albeit in a much less formal manner than Connell and Slatyer (1977). The first is replacement succession which is essentially the facilitation pathway described above. The second is direct succession in which species reestablish themselves directly after a disturbance without any intermediate stages. This seems to be common in extreme environments such as deserts and tundra. This pathway is a useful addition to the set described by Connell and Slatyer. Whittaker and Levin also described "cyclic successions," and although their meaning is not fully clear, they seem to be referring to cycles such as those driven by

recurrent fire in the chaparral. This succession type, along with the fourth type which is mosaic succession, is not strictly a type of pathway as defined by Connell and Slatyer, but instead refers to the interaction of recurrent disturbances with the basic set of pathways. This is an important extension of the scheme of Connell and Slatyer, and it is discussed later. Whittaker and Levin also mentioned plateau stages in succession which are essentially examples of the inhibition pathway described above. They emphasized the importance of the frequency and intensity of disturbance in determining the appearance of the landscape. Although they did not suggest a formal way of incorporating disturbances into a successional scheme, they did suggest that "climax, semiclimax, longer-lived successional, and fugitive species...form a continuum of which the principal axes are longevity, tolerance for reproduction in an occupied environment, and dispersibility." These axes will be discussed later in describing the successional scheme proposed by Noble and Slatyer (1980).

Horn (1976) has described three pathways in the course of his discussion of the application of Markov models to succession. He described 'obligatory succession' which is equivalent to the facilitation pathway of Connell and Slatyer (1977) and the classical pathway of Clements (1916). His "competitive hierarchy" is equivalent to the tolerance pathway of Connell and Slatyer. The third pathway is "chronic, patchy disturbance" in which the deaths of individual organisms are frequent and localized, and interactions between species take the form of a race for occupancy of the vacated site, rather than direct competitive interference. Horn suggested that this type of succession may be important in tropical and subtropical forests. Webb and others (1972) and Knight (1975) have shown that recent openings can be invaded by a variety of species including those species characteristic of old forests.

In these various descriptions of alternative successional pathways, all authors have emphasized that a combination of pathways can occur in a particular successional sequence. This, of course, makes the elucidation of the various pathways in real successional examples very difficult. In some cases an interpretation of the replacement sequences observed can be sought by examining the processes involved in the displacement of one species by another. An observer can seek examples of or perform experiments to see whether a species is facilitated, inhibited, or unaffected by the presence of other species, or whether a species has a high propensity for self-replacement. Recognition of alternative pathways in succession allows these sorts of questions to be asked; but, as can be seen from figure 1, a general scheme incorporating all the observed pathways is lacking. Egler's (1954) initial floristic composition hypothesis is a statement about the way in which establishment, competition, and replacement occur, rather than a description of an alternative pathway. Elements of Egler's hypothesis can be incorporated in the other models.

A second major shortcoming is that all the pathways depicted in figure 2 describe the succession after a single disturbance, and give little idea of the effect of subsequent disturbances on the path of succession. This aspect will be discussed later in describing the scheme of Noble and Slatyer (1980).

In reviewing the pathways proposed above, it can be argued that there are three basic pathways and these correspond to those described by Connell and Slatyer (1977). The direct succession of Whittaker and Levin (1977) can be seen as a compacted form of any one of the three major pathways; while the chronic succession of Horn (1976) is essentially a statement that any species can be followed by any other, and therefore invalidates the most commonly accepted definitions of succession which assume some directionality or predictability.

The three basic models are derived from three different views of the way in which communities are organized. The facilitation model implies either a primary succession in which direct environmental modification is essential before certain species can establish, or that a high degree of community organization exists. Odum (1969) argues

this exists and that the strategy of succession is equivalent to that of the biosphere; namely, increased homeostasis with the physical environment. However, this seems to be an argument based more on analogy with the ontogeny of organisms than on evidence, and has been criticized as such by many authors (Drury and Nisbet 1973, Colinvaux 1973, Horn 1974, Connell and Slatyer 1977).

The tolerance model emphasizes the role of competition in forming the community. Early successional species will dominate in a community only if they establish earlier than the later successional species. Inevitably these species will be outcompeted and replaced by species more efficient at exploiting resources. Connell (1975) argues that competition is not as important in community development as is often assumed. This point will be discussed below, but it is of interest to note that Connell and Slatyer (1977) could find few convincing examples of this pathway.

The inhibition model deemphasizes the role of competition, and emphasizes that, once an individual secures a space, it can resist the invasion of other individuals. Local disturbances, such as pest damage, blow down etc., are important in providing opportunities for displacements to occur, and the "climax" community will be as much dependent on the relative resistances of species to these disturbances as on their competitive abilities.

In summary the Connell and Slatyer (1977) scheme recognizes the importance of opportunist species in initially establishing at a site, but proposes that the replacement of these opportunists can proceed in one of three ways.

SPECIES ATTRIBUTES

A number of authors have sought to provide a classification of attributes which are important to the role a species plays in a particular community process. For example, Gill (1975, 1977, and this volume), Naveh (1975), and Lyon and Stickney (1977), among others, listed the attributes which are important to species which occur in areas subject to recurrent fires. Such classifications are useful in comparing vegetations subject to fires in various parts of the world, and discussing the selective pressures and adaptive significance of these characters. However, the lists do not provide sufficient information to derive descriptions of the vegetation dynamics at a site.

Noble and Slatyer (1980) (see also Noble and Slatyer 1977), sought a small number of characteristics which are vital to the role of a species in a vegetation replacement sequence (vital attributes). In doing so they attempted to find a set of attributes which is the smallest, comprehensive set needed to describe the behavior of a species in the vegetation dynamics at a site subject to recurrent disturbances. Their approach differs from the descriptions of succession described earlier in that it does not attempt to describe any underlying scheme or major evolutionary trends in community development. However, the set of vital attributes may form a useful basis for discussion of evolutionary trends, and the scheme is briefly described below. Throughout the discussion, the disturbance is assumed to be recurrent fire.

Vital Attributes

The Noble and Slatyer (1980) scheme deals mainly with succession in terrestrial, higher plant communities on a particular site with a stable physiographic climate (i.e., secondary succession). Three main groups of vital attributes are recognized. They relate to:

- (a) The method of arrival or persistence of the species at a site during and after a disturbance.

(b) The ability to establish and grow to maturity in the developing community.

(c) The time taken for the species to reach critical stages in its life history.

There is similarity between the three vital attribute groups, and the three principal axes of Whittaker and Levin (1977) which were mentioned above. Whittaker and Levin's longevity is included in (c) above; "tolerance for reproduction in an occupied environment" is essentially (b); and "dispersability" is incorporated in (a).

In attempting to form a classification of important successional properties of a species, the scheme differs from the usual emphasis on the stochastic aspects and multiple mechanisms involved in vegetation dynamics (Horn 1974) by assuming that there are limited adaptive possibilities to any environment (Mooney 1974). The Noble and Slatyer scheme seeks to utilize this by emphasizing not the mechanisms leading to various behavior patterns (Gill, in this volume), but rather the outcome of these mechanisms. In moving towards a classificatory approach, their scheme also differs from the emphasis on gradient analysis (Pickett 1976). However, both the classificatory and continuum approaches are simply models of the real world and as Watt (1947) stated, "The formulation of laws and their expression in mathematical terms, will be facilitated if an acceptable qualitative statement of the nature of the relations between the components of the community is first presented." The vital attribute approach attempts to provide a qualitative statement about the major processes involved in vegetation sequences, and in doing so, to form a basis for further quantitative elaboration, or alternatively, for further logical analysis of the processes involved in community change (for example, via grammar theory, Haefner 1978).

The first step in the Noble and Slatyer (1980) scheme is to recognize four major life stages in the population of a species. These are the juvenile stage, when the majority of the individuals of the population of a species at a site are immature; a mature stage, in which the majority are mature (but juveniles may still be present); a propagule stage in which the species is not present as juveniles or adults, but only as a store of propagules (seeds, bulbs, dormant root stocks, etc.) and a locally extinct stage when all traces of the species are absent. These stages form the basis for the derivation of the vital attributes of the species.

In the full description of the scheme, Noble and Slatyer (1980) examined patterns of availability of a persistence mechanism in relation to the above life stages, and they concluded that only 10 vital attributes related to the method of persistence are biologically feasible. These 10 vital attributes are described by way of examples in table 1, and their relationship to the life stages (which is the basis of their strict definition) is shown in figure 3. It is important to emphasize that the vital attributes are based on the outcome of mechanisms and not the mechanisms themselves. For example, a species with widely dispersed seeds (e.g., animal dispersed hard fruits) will often have some seed stored in the canopy and, therefore, is similar to species classified as C. However, the outcome in terms of the pattern of availability of a method of persistence is still that of D (fig. 3).

The second group of vital attributes describes the conditions in which a species, which has propagules available at a site, can establish and grow to maturity. Two stages in community development after a disturbance such as fire are recognized: first, the stage immediately following a disturbance during which there is often little competition for resources, and later, the stage when competition for resources becomes increasingly important as the community closes. The three vital attributes recognized by Noble and Slatyer (1980) are described in table 2.

Noble and Slatyer (1980) defined a "species type" which is based on the two vital attributes discussed above. For example, many fireweed species are of species type

TABLE 1.--Vital attributes associated with the method of persistence during and immediately after a disturbance

PROPAGULE BASED

- D Species with highly dispersed propagules.
- S Species with a long-lived propagule store, e.g., a long-lived seed store in the soil.
- G A special case of S, in which the entire seed store either germinates or perishes at a disturbance.
- C Species with a short-lived propagule store, e.g., seed stored in the canopy.

VEGETATIVE BASED

- V Species which resprout, but which must pass through a juvenile stage before becoming mature again, e.g., a species which coppices from the stem base or lignotuber (burl).
- U Species which are virtually unaffected by the disturbance.
- W A special case of U, in which individuals at the adult stage are virtually unaffected, but those at a juvenile stage are killed.

COMBINATIONS

- $\Delta \Sigma \Gamma$ Correspond to D, S, and G except that the adult stages are virtually unaffected by the disturbance.
-

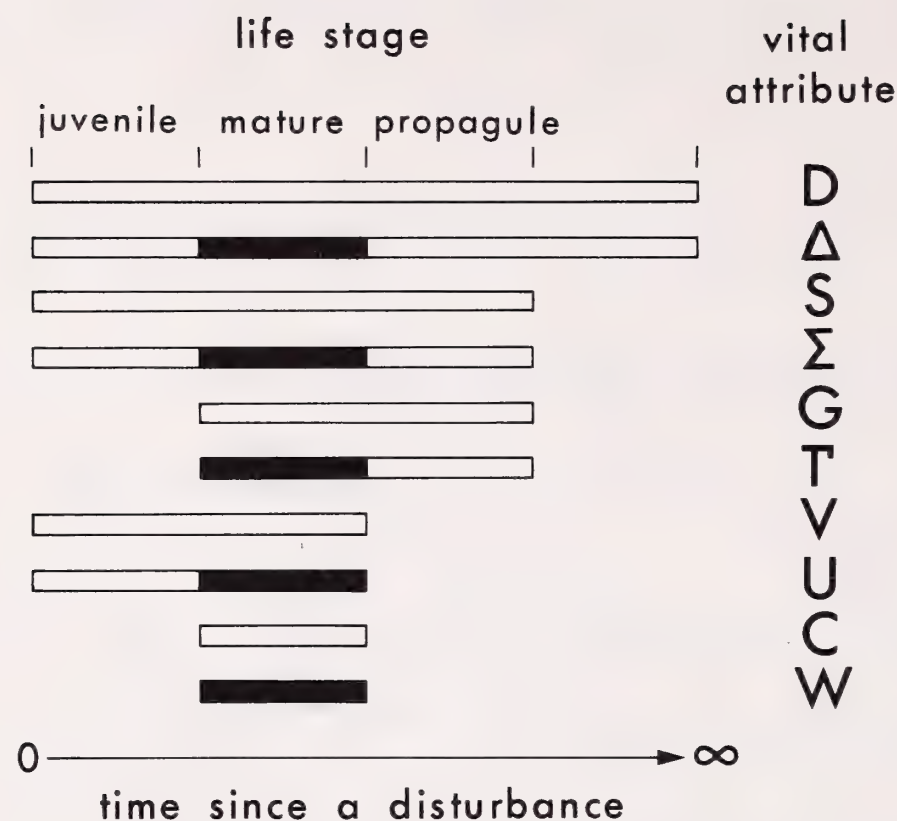


Figure 3.--A summary of the 10 vital attributes associated with the method of persistence. An open bar indicates that a method of persistence is available at a particular life stage of a species population. The method will usually result in only juvenile material being present immediately after a disturbance, but in some cases (solid bar) mature tissue will persist.

TABLE 2.--Vital attributes associated with the conditions for establishment.

T	Species which can establish and grow to maturity both immediately after a disturbance and for an indefinite period thereafter (i.e., <u>t</u> olerant).
I	Species which can establish only immediately after a disturbance (i.e., <u>i</u> ntolerant).
R	Species which cannot establish at the site immediately after a disturbance, but can do so some time later (i.e., they have some requirement which must be filled, e.g., shade, before they can establish).

D, since they have widely dispersed seeds, but can only establish at a recently burned site; many rain-forest species are of species type CT since they have only a short-lived seed store, but can germinate and establish independently of a disturbance. Although 30 species types may be derived from the vital attributes, Noble and Slatyer show that only 15 distinct behavior patterns in vegetation replacement sequences occur.

The third group of vital attributes describes the timing of important events in the life history of the species. The life stage parameters appropriate to each species type are shown in figure 4. The parameters are the time taken to reach reproductive maturity, the longevity of the species and the longevity of the propagule store. These parameters are related to the population of the species and not to individuals. Therefore the longevity of a tolerant species is effectively infinite since it will retain a self-regenerating population in the absence of a disturbance, while the longevity of an intolerant species is approximately the life span of the individuals comprising the population.

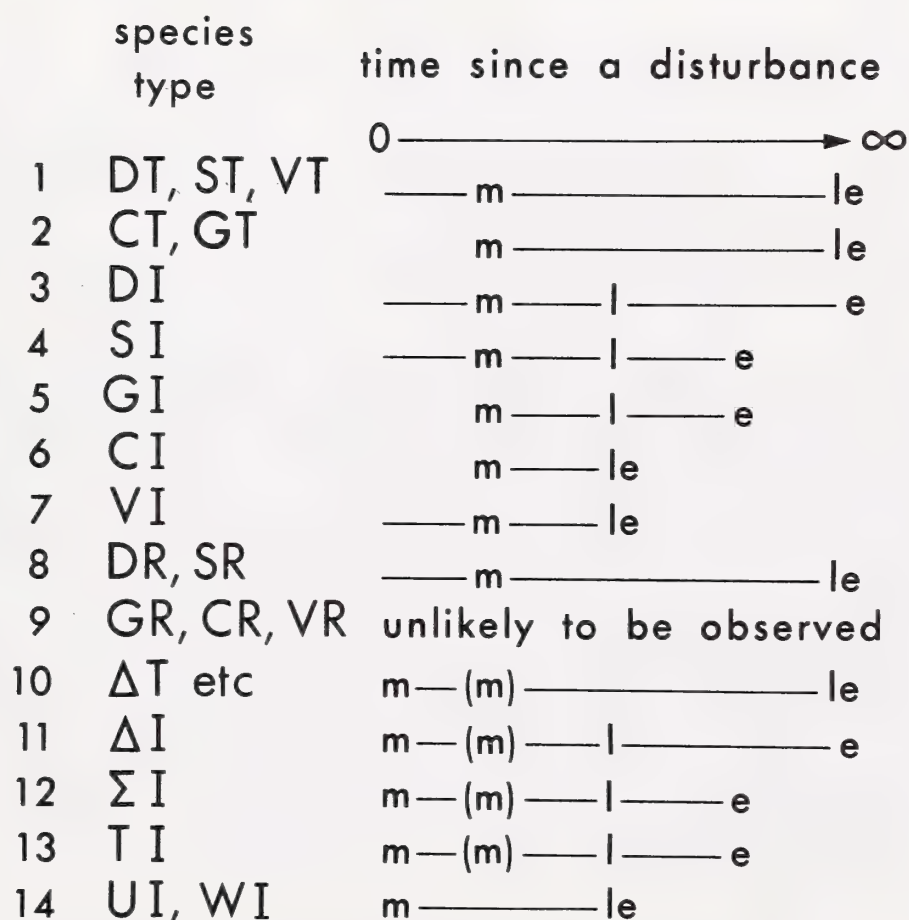


Figure 4.--Life stage parameter characteristics for each of the species types. The species types are grouped on the basis of similar patterns of behavior in replacement sequences. The critical events are the time to reach reproductive maturity (m), the longevity of the species population (l), and the longevity of its propagule pool (e).

A very simplified example of the application of the vital attribute approach is given in figure 5, where a replacement sequence for a hypothetical open woodland-savanna community dominated by a tree species (e.g., an *Acacia*) and a grass understory is derived. For the purposes of the example it is assumed that the tree is an obligate seed regenerator which reaches reproductive maturity at 10 years, has a life span of 80 years, and retains viable seed in the soil for 40 years after the death of the adult. The tree will only become established after a disturbance, such as fire, when all or most of the seed pool will either germinate or perish as a result of the fire. The tree is therefore classified as a GI species type. The grass reaches maturity after 1 year and, although individuals may have a short life span, they have widely dispersed seeds which can become established at any time. The grass is therefore of species type DT.

The replacement sequence in figure 5 shows, at the top, a summary of the vital attribute data for the two species. The replacement sequence derived from the summary shows that if both species are present as juveniles after a fire, then after 1 year the grass matures and after 10 years so does the tree species. If fire does not occur for 80 years the tree individuals senesce and die, but the seed pool remains for another 40 years, so that after 120 years the tree will become locally extinct. The transitions in undisturbed situations are shown by the unbroken arrows.

The effect of fire is shown by the dashed-line arrows. If a second fire occurs before the tree species has reached maturity (10 years), then the seed pool of the tree species will not have been restored and therefore little regeneration of the trees will occur, and the tree species effectively will be locally extinct. If a second fire occurs between 10 and 120 years, the seed pool will exist and both species will reestablish. A period of 120 years without fire will result in the local extinction of the tree species since the seed pool will no longer be viable.

This simple example serves to show that the vital attribute data summarized at the top of figure 5 is sufficient to derive many of the details of vegetation dynamics under recurrent disturbance. Depending on the fire regime, it is apparent that the relative abundance of trees can fluctuate in this community, and a pure grassland can result under specific fire frequencies. Figure 6 shows a more realistic example based on the temperate rain forests of Tasmania (see Noble and Slatyer 1980 for a full description). The vital attribute data for the four species allows the "classical successional sequence," from wet sclerophyll to mixed forest to rain forest, to be derived, but also leads to several alternative pathways which result from particular fire regimes. Although this scheme seeks to impose a classificatory approach in a clearly continuous situation, the vital attribute data, and especially the species type, summarize many of the processes important in the role of a species in vegetation dynamics; and therefore it may be of value to look at the vital attribute scheme in evolutionary terms, and in particular at the role of fire frequency in selecting for different species types.

Evolutionary Aspects of Vital Attributes

Short-viability propagules, which are stored in a way that they can survive a disturbance such as fire (C vital attribute), represent a simple method of persistence. This method requires no specialized propagule dispersal or long-term storage mechanisms and no resprouting ability. However, species with the C vital attribute can persist at a site subject to only a limited range of disturbance frequencies. An interfire period shorter than the time taken for a species to reach maturity usually results in the local extinction of the species. The method of persistence is only available while adults are present at a site, and, therefore, although adults of CT or CR species may continue regenerating at a site indefinitely, CI species become locally extinct at the senescence and death of the population.

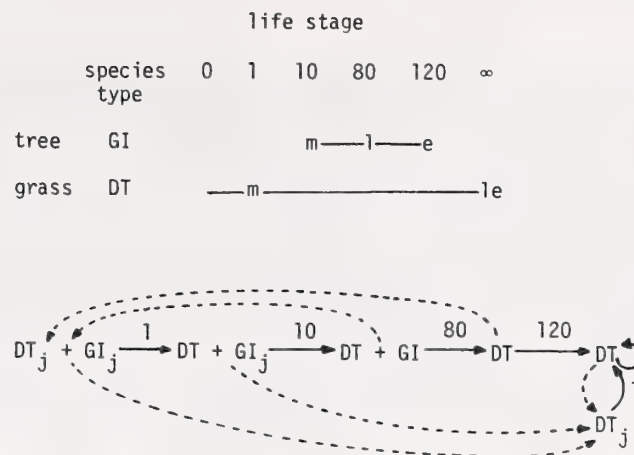


Figure 5.--A hypothetical replacement sequence derived from the vital attribute data shown at the top of the figure. A full description is included in the text.

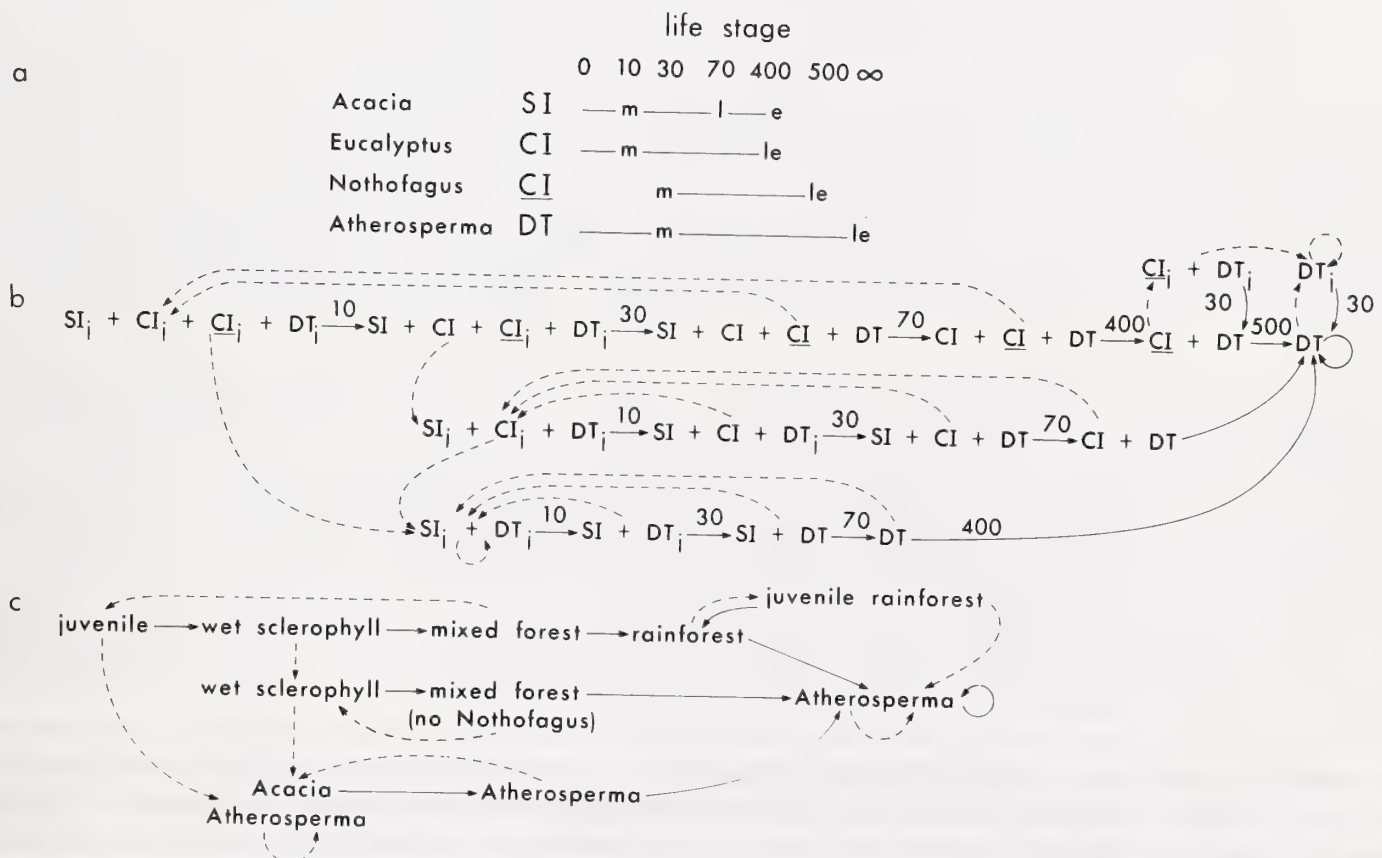


Figure 6.--The vegetation replacement sequence for the Tasmanian wet sclerophyll - rain forest system (from Noble and Slatyer 1980). 6a. - A summary of the vital attribute data used to derive the sequence shown in 6b. (The underlined CI is used to distinguish Eucalyptus and Nothofagus in replacement sequence.) 6c. - A summary of 6b. Solid arrows show transitions in periods with no disturbance, while broken line arrows show transitions due to fires. The numbers refer to the approximate times in years since the previous fire.

Once they have established, species with the T or R vital attribute can persist at a site for an indefinitely long period between disturbances and they therefore seem to be at an advantage over I species. However, an important property of species with the T or R vital attribute is the capacity to tolerate shade, especially during the seedling stage. It appears that shade tolerance is correlated with low photosynthetic rates (see Leopold and Kriedeman 1975) and low metabolic rates in general (Grime 1965). Changes in the grana structure and photosystem II activity are associated with shade tolerance, and, although many species show a large degree of plasticity in producing either sun or shade leaves, tolerant species do seem to be at a disadvantage during growth in unshaded conditions when compared with intolerant species.

Therefore, CT and CR species may be expected to be successful in situations where the interdisturbance period is rarely very short and is often very long, while CI species are restricted to sites with a narrow range of disturbance frequencies. This is reflected in many rain forest species being of species type CT while CI species appear to be common in heath situations (Noble and Slatyer 1977). In these sites, interfire periods are usually much shorter than the life span of the CI species. The fires also tend to be intense and consume most of the fuel and therefore subsequent fires are rare until fuel builds up. During this period the CI species can reach maturity.

Species with the G vital attribute have long-lived propagules which extend the longest interfire period through which they can persist. This is of no advantage for GT or GR species over CT or CR species. Usually some increased energetic cost is involved in producing long viability seeds. The role of predation is also important: Whereas C species often retain their viable seeds in the canopy, G species usually release their seeds at some stage and therefore are subject to both canopy seed predators and ground level seed predators. The main advantage of the G over the C vital attribute (for all of GI, GT, and GR) is that greater seed accumulations can occur in a long-viability seed store than in a short-viability store. This means that less resources each season need be diverted to the seeds themselves thus leaving more resources for the survival of the parent or for additional protection of the seeds produced.

Despite these advantages, examples of the G vital attribute appear to be rare. The reason becomes clear when the G and S vital attributes are compared. The S vital attribute is identical with the G vital attribute except that in the former not all the propagules germinate or perish when a disturbance occurs. This means that species with the S vital attribute can persist through occasional short interfire periods by drawing on the residual propagule pool. Many species have evolved great plasticity in germination response, and, since there appears to be no major disadvantage associated with this adaptation, most species with a long-lived propagule store show the S vital attribute. Many understory shrubs in fire-prone forests and woodlands are of species type SI. Long life spans, coupled with long seed viability--possibly centuries in the case of some Australian *Acacia* species (Gilbert 1959)--enable these shrubs to survive long interfire periods, while the residual seed pool enables them to persist through fires which may occur in the fuels (mainly grasses and small shrubs) that build up before the SI species reach reproductive maturity. Examples of species type ST seem to be rare, although this may be because it is difficult to distinguish ST species from CT species unless a short interfire period occurs, or unless the method of seed storage is known. Unfortunately seed storage is a poorly studied field (Harper 1977).

Species with the D vital attribute have highly dispersed propagules and, provided there is an adequate mosaic of disturbances near the site to provide sources of mature individuals, these species have propagules available at all times. This would seem the ideal method of persistence; however, several disadvantages are associated with dispersal. The plant must often divert production into dispersal aids such as wings, floats, or attachment mechanisms in passively dispersed species, or into dispersal-agent

attractors in actively dispersed species. Since dispersal is essentially a wasteful method of persistence with large numbers of propagules being destroyed or deposited in unfavorable sites, diversion of production away from the propagules themselves is costly in evolutionary terms. The other disadvantages relate to the risks of predation and wastage due to deposition on unfavorable substrates (which usually ends up in predation). Since dispersal is risky, there is an advantage in producing large numbers of propagules, and this in turn can lead to selection pressure to produce small propagules. However, small propagules are often at a competitive disadvantage during germination and establishment and a balance between size and number needs to be retained. Therefore, although dispersal is a viable method of persistence, for all types of disturbance regimes, it is not surprising that other methods of persistence have remained important in situations where the disturbance frequency is relatively regular.

Nevertheless species with the D vital attribute do occur in a wide range of situations. For example, many early pioneer species and "fire weeds" are DI species. These species are usually small in size, with rapid growth rates and short life spans. A large proportion of their production is allocated to reproduction and dispersal. They are typical r-species, exploiting sites which are only ephemerally available, or alternatively they may be thought of as exploiting situations where the interfire period at a particular site is very long with respect to their life spans. Some rain forest trees appear to be DT species, even though it seems unusual that a tolerant species in a relatively infrequently disturbed habitat should have evolved a wide dispersal mechanism. This may arise from several selection pressures. High seed and seedling predation rates, especially near parent trees (Janzen 1970), will select for increased dispersal characteristics. Also the scarcity of gaps suitable for regeneration in a rain forest will lead to the selection for individuals with wide dispersal powers which therefore have more recruitment opportunities. A similar selection pressure may have led to the existence of DT species as late successional species in temperate forests. Many of the late successional species in North American temperate forest (e.g., beech, larch, sugar maple) appear to persist through disturbances via dispersal (Noble and Slatyer 1980). The DR species type is common in commensal and parasitic species. For example, mistletoes are distributed widely by birds, but dispersal and reestablishment at a disturbed site can only occur after some tree regeneration has taken place.

The discussion above has centered on methods of persistence based on propagules. The alternative method is via vegetative persistence. The discussion of the evolutionary aspects of vegetative methods of persistence is made difficult since vegetative propagation may be seen as a method of increasing the longevity of an individual, as in the case where a damaged individual simply resprouts and regrows to its original form. Alternatively, it may be seen as a method of asexual reproduction when an individual gains a larger share of resources by spreading or dividing as a result of vegetative regeneration.

Vegetative regrowth is usually associated with "equilibrium" species in predictable environments (Harper and others 1970); however, it is necessary to distinguish between vegetative spread by layering or root sprouting, etc., and vegetative resprouting (sometimes associated with spread) following a disturbance. The former is an example of the T vital attribute.

Vegetative regrowth is common in fire-prone environments. Wells (1969) argued that in chaparral species sprouting is a relatively primitive character and that obligate seed regeneration is a result of the loss of this character. Many chaparral species (as with species of heath, marquis, etc.) are VI species. Some species do show significant seedling regeneration after fire as well, but the outcome of both the sprouting and the short-term seed store is still the V vital attribute (fig. 3). It appears that VI species are at an advantage over CI species in fire-prone environments

since they are not at risk from short interfire periods. Keeley and Zedler (1978) make this same point, but point out that the increased outbreeding due to obligate seed regeneration leads to increased genetic diversity and the ability of seedlings to establish in the highly variable seasonal conditions following a fire. Obligate seed regeneration tends to be favored by longer interfire periods.

One of the most outstanding examples of VI species is the genus Eucalyptus which dominates the tree (and much of the shrub) flora of Australia. All are VI species except a small number of wet sclerophyll forest species which are CI species. This is possibly a reflection of the frequency of fire over large portions of Australia. Eucalyptus species which have lost their capacity to sprout from stems and stumps are found only in wet forests where short interfire periods are uncommon.

VT species have great potential to persist and dominate since they are able to regenerate immediately after a fire from vegetative reserves and therefore often have a competitive advantage over seedlings; and, having regenerated, they can persist indefinitely. Some examples confirm this "super-species" label. Some are understory species, such as bracken (Pteridium aqualinum) which can cover large areas to the exclusion of most other species. Other examples include the Imperata grasslands of the tropics which can dominate large areas to the exclusion of other life forms (Whitmore 1975). Similarly many thicket species such as bamboo are VT species.

The remaining vital attributes associated with the method of persistence (i.e., U, W, Δ , Σ , and Γ) will not be discussed here. These vital attributes all involve situations where adult individuals survive a disturbance effectively unharmed as can often occur in mild fires. Noble and Slatyer (1980) have discussed the role of disturbance intensity in their scheme and I will not deal with it here.

Table 3 presents a summary of the discussion of the relationship between species type and the range of interfire intervals experienced at a site. Short interfire intervals are those cases where a second fire occurs before individuals regenerating from an earlier fire reach reproductive maturity, while interfire intervals greater than the life span of individuals of the species are regarded as long. The interfire period is measured with respect to a particular species; for example, Eucalyptus and Acacia species can occur at the same site which has occasional short interfire periods. However, interfire periods longer than the life span of the Acacia species (about 50 years) may be common, while interfire periods longer than the life span of the Eucalyptus species (about 300 years) may be rare. Therefore, the SI and VI species types represent alternative responses to the same disturbance regime.

Herbivory often plays a significant role in vegetation dynamics. The introduction of a source of predation can modify the vital attribute description of some species. The most extreme, but trivial, example is where grazing causes the total destruction of the adults and any regrowth of the species. This will eventually lead to the local extinction of all but D and Δ species, although some seed pools may remain for a long time. Predation which prevents reproduction alone, can eventually lead to local extinction of most species, and this process can be hastened by fire.

Herbivory can modify the vital attributes in a more subtle way than described above. For example, a T species may be altered to an I species by the introduction of an herbivore which prevents reproduction under normal circumstances, but which does not prevent regeneration and reproduction after a disturbance. This can occur if the species reestablishes prolifically after a fire, or if the herbivore prefers unburned sites and temporarily leaves the burned area. A T species may act as an R species if, after a fire, individuals are prevented from reestablishing due to heavy grazing pressure; but, as the community recovers, grazing pressure is reduced and establishment again becomes possible. Grazing pressure may be reduced due to the protection afforded by other individuals, or to the herbivore altering its diet to other species or other areas. A species classified as an I species in sites unaffected by the herbivore can

TABLE 3.--Summary of some species types and the interfire periods to which they are adapted

Species type	Short	Long	Examples
	(<maturity)	(>life span)	
CT,CR	rare	often	rain forest species
CI	rare	rare	heath species
SI	occasional	often	<u>Acacia</u>
VI	occasional	rare	<u>Eucalptus</u>
DI	rare (but mosaic pattern, cf. Keeley, this volume)	often	fire weeds
VT	any periodicity		pyric grasslands, bracken

act as a T species under the influence of grazing. This occurs if the herbivore opens gaps in the community which provide microhabitats for the species to regenerate. Other such transitions are possible, and it must be recognized that in many regions herbivory and recurrent fire have both played a major role in shaping the existing vegetation (e.g., Naveh 1975). Many adaptations observed in species are probably a response to the loss of aboveground tissue, whether this be by grazing or burning. However, the two processes are not equivalent and changing the intensity and frequency of either will affect community structure since there is no necessary correlation between palatability and fire sensitivity and hence different species are favored or harmed by each process.

The above discussion shows that fire frequency has a major influence on the types of strategies which are successful at particular sites. The scheme proposed by Noble and Slatyer (1980), and especially this discussion of it, places great emphasis on the method of persistence and initiation of regeneration after a disturbance and less on the subsequent growth and competitive interactions. This is mainly because in situations subject to recurrent disturbances such as fire, events requiring persistence and regrowth occur frequently and the competitive interactions of the adults often do not have time to play themselves out before another fire occurs. The role of competition and its modification by predation in community organization have come under scrutiny recently. Several authors (Connell 1975, Grubb 1977) have criticized the emphasis placed on competition in determining niche structure, niche packing, and species diversity (Hutchinson 1958, Vandermeer 1972).

COMPETITION, PREDATION, AND THE REGENERATION NICHE

Connell (1975) questioned whether competition is the sole or even principal mechanism which determines the realized niche of a species. Connell emphasized he was concerned mainly with the distribution of the species and not its population size. This same emphasis occurs in the Noble and Slatyer (1980) scheme, where species are recognized as present or absent from a site, and no predictions of population size, dominance, or other measure of local importance are considered. Connell argued from experiments and observation of plants and animals that many species rarely reach population densities great enough to compete for resources. Instead, physical extremes

and predation (taken in its broadest sense) acting on the young stages reduce population sizes and maintain them below levels at which competition is important. Young (i.e., small) individuals are considered by Connell to be more subject to mortality due to both physical extremes and predation. He sees selection pressure leading to either increased size or, in those cases where size is an inadequate defense against predation (e.g., as with trees subject to invertebrate grazers, or micro-organism attack), to increased refuging.

Studies of Eucalyptus communities in the Snowy Mountains of Australia by Morrow (1977) give an interesting insight into the effects of predation in a community. Morrow concluded that, in the absence of predation, Eucalyptus stellulata has higher growth rates than the predominant tree in the region, E. pauciflora. However, E. stellulata is subject to more insect grazing than E. pauciflora and Morrow concludes that E. stellulata is thereby prevented from competitively excluding the slower growing species. However, her study does not show whether E. stellulata can displace E. pauciflora in the absence of insect grazing. This seems unlikely since the area is subject to recurrent fire, with sites being burned every few decades. During the interfire periods there is little mortality, indicating that, if competition is occurring, it is not leading to any strong selection of either species. The recurrent fire means that the period of regeneration is of major importance. It is at this stage that physical extremes and fluctuations in grazing intensity can affect the survival of the resprouting Eucalypts and of their seedlings.

Grubb (1977) has proposed that much greater importance needs to be given to the regeneration stage in plant communities. He pointed out that many botanists find "Gause's hypothesis" untenable since there appears to be insufficient niches "explained" in terms of light, carbon dioxide, water, and nutrients. This arises because of the failure to consider the regeneration process in plant communities. Grubb sees "almost limitless possibilities" for differences between species in their requirements for seed production, release, and dispersal, and for germination, establishment, and onward growth. Species may coexist indefinitely on the basis of a difference in regeneration niche, even when one species will oust another if they are matched against each other for a long period, providing sufficient regeneration opportunities occur for the weaker species. If the regeneration niche is a major factor in determining community composition, then this is important in vegetation studies; since observations of mature vegetation will often not be sufficient to distinguish the events which occurred during regeneration, and which gave the vegetation its existing character.

CONCLUSION

The concept of the regeneration niche is particularly important in considering secondary succession after fire. Recurrent fires lead to the frequent creation of major regeneration events and reduce the time span over which competitive interactions of mature individuals can take place. Changes in fire frequency induced by human activity can alter the relative importance of these two stages in determining community structure and organization. This review has described a change in successional thinking from an emphasis on community processes to an increased emphasis on species' properties and in particular on the regeneration niche of the species.

This review is a reflection of a particular set of biases. I have not dealt with such questions as whether early successional species have better defense against predators than late successional species. Cates and Orians (1975) suggested, and found supporting evidence using slugs, that early successional plants should invest relatively little of their resources in defense against herbivores, but should instead divert most of their resources to growth and reproduction. However, Root (1975) has suggested that early successional plants should produce more defenses against

herbivores since they cannot rely upon their large size (cf. Connell 1975) as a protection against predation. Otte (1975), using grasshoppers, found evidence to support Root's hypothesis. Whittaker and Levins' (1977) warning about generalizations becoming confused into increasing numbers of exceptions and complications seems appropriate here. However, we cannot afford to relegate succession to the "too hard basket." I have attempted in this review to show that a reemphasis of autecological studies with special emphasis on the regeneration niche will provide the basic data we need to understand vegetation dynamics. If these data are summarized by careful generalizations and classifications (as Connell and Slatyer [1977] and Noble and Slatyer [1980] have attempted to do), it may lead to descriptions of successional processes which are useful to those who need to make decisions about vegetation management.

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PLANT NUTRIENT ABSORPTION AND RETENTION UNDER DIFFERING FIRE REGIMES

F. Stuart Chapin, III

Associate Professor of Plant Physiological Ecology
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

and

Keith Van Cleve

Professor of Forest Soils
Department of Forest Soils
University of Alaska
Fairbanks, AK 99701

ABSTRACT

Fire affects plant nutrition by altering nutrient and light availability and the competitive advantage of plants with different growth rates. As succession proceeds after fire, plants change their pattern of nutrient use through (1) an increased root-to-leaf ratio, (2) decreased nutrient uptake per unit root, (3) decreased rates of leaf and root turnover, and (4) decreased photosynthetic rate. These factors all cause slow growth. These changing patterns of nutrient use are consequences of both changing species composition and physiological changes in fire-surviving species. Plants that resprout following fire appear to have greater plasticity with respect to these characteristics than do species that replace one another in postfire succession. The interactions, relative importance, and management implications of factors relating to different aspects of plant nutrient use are discussed.

KEYWORDS: nutrient, fire, succession, adaptive strategy, uptake

INTRODUCTION

One of the principal ecological consequences of fire is the sudden release of mineral nutrients from plants and soil organic matter. These elements are either lost from the system through volatilization and smoke release or returned to the soil in available form (Grier 1975; Stark 1977; Debano and Conrad 1978; Woodmansee and Wallach 1979). After a fire, high nutrient availability permits rapid establishment and/or regeneration of the vegetation which may prevent leaching of nutrients from the system (Ahlgren 1960; Christensen and Muller 1975; Stark and Steele 1977). As the community develops, nutrients gradually become incorporated into plant and soil organic matter and are therefore less available in the soil for absorption by plant roots. Thus, the vegetation is exposed to substantial change in nutrient availability through a fire cycle. Some species survive fire and successfully compete through all the varying conditions of the fire cycle. Other species are adapted to exploit only certain successional stages and must recolonize from seed following fire.

Here we explore the nature of plant adaptations to absorb and retain nutrients and consider how these adaptations affect growth under regimes of differing fire frequency and intensity. We first consider growth form, growth rate, leaf and root turnover, nutrient uptake, and storage as separate features and then discuss their interrelationships as these change with fire regime. Our basic thesis is that plants have adapted to different resource availabilities and that fire acts mainly to alter the availability of resources such as nutrients, water, and light. The adaptations we describe are not unique to postfire succession but are found in any situation of changing resource availability.

Although the importance of changing nutrient status through a fire cycle has long been recognized, surprisingly little work has specifically addressed the nature of plant adaptations to nutrient use. For this reason we draw upon a variety of studies and experimental approaches and try to provide a theoretical basis for understanding plant nutrition in relation to fire regime.

GROWTH FORM

Christensen (this volume) emphasizes the importance of growth form in determining fire frequency. However, fire frequency in turn places constraints on the types of growth forms that are successful in a given environment. Growth forms such as trees, shrubs, and herbaceous plants differ in the time necessary to acquire the carbon and mineral resources necessary for reproduction. If fires recur more frequently than the time required for this resource accumulation, the growth form is unlikely to successfully reproduce and maintain itself. Consequently, trees are a predominant growth form only where the fire return time is relatively long. Environments with progressively shorter fire return times are characterized by shrubs and grasses, respectively (table 1; Keeley 1979). Fire return time is the average time interval between successive fires that destroy most aboveground plant parts. T_{50} is the time required for accumulation of half the maximum aboveground standing crop of biomass or nutrients found in mature steady-state stands. Although fire return time and T_{50} are determined independently, there is a clear correlation between the two, suggesting the importance of fire frequency as a selective factor in determining dominant growth form. When fire frequency is either increased or decreased as a result of man's activities, there is usually a rapid change in growth form dominance (Daubenmire 1968; Bragg and Hulbert 1976). For example, a tropical forest burned at 5-year intervals becomes shrub-dominated (Eiten 1972), as do grasslands protected from fire (Daubenmire 1968; Kucera this volume). Fire-resistant trees (e.g., longleaf pine) lose little tissue in a normal fire, require little time to replace that tissue, and are thus similar to grasses in the fire return time tolerated (Christensen this volume).

TABLE 1.--Average fire return time and time (T_{50}) required for accumulation of 50 percent of the maximum nutrient standing crop in live aboveground biomass. Values are estimated from data presented in cited references.

Ecosystem	Dominant	Fire return time	T_{50}					Ref. ^{1/}
			Biomass	N	P	K	Ca	
		Years						
Tropical tallgrass	<u>Chrysopogon fallax</u>	1.5	0.4					1
Subtropical grass-land	<u>Aristida stricta</u>	1	.6					2
Subtropical marsh	<u>Cladium jamaicense</u>	2-3	.8	0.8	0.8	0.3	0.6	3
Tallgrass prairie	<u>Andropogon gerardi</u>	<5	<1					4
Dry heath	<u>Calluna vulgaris</u>	12	12	8	7	11	8	5
Chaparral	<u>Adenostoma fasciculatum</u>	15	15					6
Coniferous forest	<u>Pinus banksiana</u>	60		21	24	21	21	7

- ^{1/}
- | | |
|---------------------------------------|---------------------------|
| 1. Smith 1960 | 5. Chapman 1967 |
| 2. Hilmon and Hughes 1965; Lemon 1949 | 6. Conrad and DeBano 1974 |
| 3. Steward and Ornes 1975 | 7. MacLean and Wein 1977a |
| 4. Kucera and Ehrenreich 1962 | |

Environmental factors such as temperature, moisture, and nutrient availability also clearly affect the rate at which each growth form acquires resources and therefore affect the growth form that can be supported under a given fire frequency regime. As these factors become more favorable for growth, a larger growth form can be supported at a given fire return time (fig. 1). Moreover, other disturbances such as grazing may be as effective as fire in favoring dominance of small-biomass growth forms (Kucera this volume). In view of these complicating factors, the correlation between fire return time and T_{50} (table 1) is surprisingly good.

GROWTH RATE

Competition for light and nutrients increases through succession in general and through postfire succession in particular. Early in postfire succession rapid growth, which depends upon abundant resources, is advantageous. Later in succession such resources may be less available, and those plants with inherently high growth rates and resource requirements may not survive (Grime and Hunt 1975; Grime 1977). Thus, different inherent relative growth rates are adaptive at different points in the fire cycle.

There are many lines of evidence indicating that relative growth rate (i.e., growth rate in proportion to biomass) changes through a fire cycle. If we look at entire communities, we see that plant productivity increases exponentially immediately following fire but eventually declines as some equilibrium biomass is approached (Chapman 1967; Odum 1969; Vitousek and Reiners 1975). This indicates slower relative growth rate in late succession, due both to the high expenditure of carbon in maintenance of living but nonproductive tissues and to decreased mineral availability to support further growth.

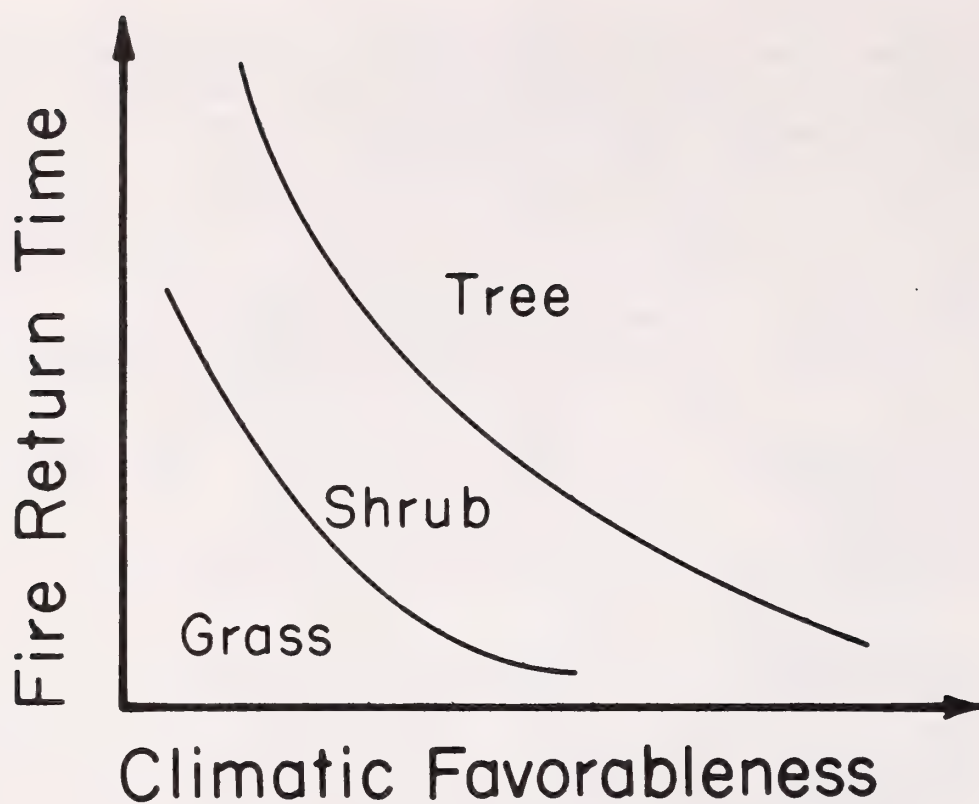


Figure 1.--Diagrammatic relationship between fire return time and environmental factors (e.g., moisture, temperature, and soil nutrient availability) influencing growth as these affect plant growth form. Isolines show points of equal aboveground biomass.

Change in relative growth rate through postfire succession can be seen in individual species as well as entire communities. Early postfire successional species characteristically have high relative growth rates. As competition becomes more intense, light, minerals, and perhaps water are no longer sufficient to support the high growth rate. The growth rate of these species then declines, becomes negative, and the species is eliminated. Thus, species with inherently high relative growth rate and resource requirements are less successful in late succession (Grime 1977; Noble this volume). Late fire-successional species seldom exhibit the high relative growth rate of early invaders. Their low relative growth rate puts them at a disadvantage in early succession, but because of their tolerance of low annual resource availabilities, these species maintain a positive relative growth rate even in late succession and eventually become dominant (Grime 1977; Connell and Slatyer 1977).

Species that resprout following fire are characterized by large changes in productivity and relative growth rate through a fire cycle. It is because of this extreme plasticity in relative growth rate that fire has become such an important management tool in controlling productivity of fire-surviving species. By burning, relative growth rate and productivity are generally enhanced, although frequently repeated burning may reduce nutrient availability and reduce production. Reserve storage and release from competition are major reasons for the large change in relative growth rate observed in fire-resprouting species. Immediately following fire, regrowth is supported by stored carbohydrate (and perhaps nutrient) reserves as well as by current photosynthate, so that growth is more rapid than would be expected if new leaves were the sole source of carbohydrate (Schier and Zasada 1973). As the plants mature, some photosynthate is diverted from production to storage and is therefore unavailable for growth.

LEAF AND ROOT TURNOVER

Rates of leaf turnover may decrease through succession after fire due to changes in availability of environmental resources and changing species composition. This is an important factor explaining the differences in relative growth rate discussed above. Deciduous plants generally have higher photosynthetic rates than evergreens in the same environment, and photosynthetic rate declines with leaf age in mature leaves (Mooney 1972; Johnson and Tieszen 1976), so that a reasonably rapid leaf turnover (e.g., annual) should maintain high rates of carbon gain and rapid growth and therefore provide competitive advantage in a favorable environment (Mooney and Dunn 1970; Orians and Solbrig 1977). However, such rapid leaf turnover increases the nutrient requirements for growth. Plants may retranslocate some soluble nutrients and organic compounds before a leaf or root is shed, but the efficiency of this retranslocation is limited. No calcium is retranslocated, and approximately 40 to 60 percent of the maximal nitrogen and phosphorus invested in a leaf may be retranslocated (Goodman and Perkins 1959; Gauch 1972; Chapin and others 1975). Thus species with rapid tissue turnover have continual high nutrient requirements for the production of new leaves. Such high turnover species should be favored where nutrients are more readily available.

Early postfire species are characteristically deciduous, whereas in many communities evergreen species with their slower leaf turnover become more evident later in succession (Viereck 1973; MacLean and Wein 1977a). Within the evergreens, leaf turnover rate tends to decline as the community matures. For example, in central Alaska Picea mariana retains its needles for an average of 3 to 7 years as a seedling invading a burn but keeps them an average of 30 years in a 120-year mature stand.

Grime (1977) and Orians and Solbrig (1977) on differing theoretical grounds suggest that species with high leaf turnover also have rapid root turnover. Our observations in the taiga support this generalization. For example, the major taiga deciduous trees (aspen, birch, and larch) have relatively few roots that survive the winter whereas the evergreen species (black and white spruce) have many highly active roots that are at least 1 year old (Chapin, unpubl.). Thus we expect rate of root turnover to decline through postfire succession as a result of changing species composition and probably as a phenotypic change in resprouting species.

NUTRIENT ABSORPTION

In order to support the observed rapid growth and tissue turnover rates characteristic of early postfire vegetation, plants must maintain substantial rates of nutrient uptake. Nutrient uptake by postfire vegetation can minimize nutrient loss to adjacent watersheds following fire (McColl and Grigal 1977; Wright this volume). If a fire is sufficiently hot to burn off most vegetation, nutrient losses to ground water are greater than in sites where plants survive fire (Stark 1977). A variety of factors affect nutrient uptake by the vegetation, such as nutrient availability, absorption rate per root, and root biomass. The relative importance of these factors through succession is not immediately evident. We will consider each factor individually.

Nutrient Availability

The most obvious factor favoring rapid nutrient uptake by plants following fire is high nutrient availability in the soil. This has been frequently documented and need not be discussed in detail in the context of plant adaptations (Steward and Ornes 1975; Christensen and Muller 1975; Christensen 1977; Stark and Steele 1977; DeBano and Conrad 1978; Woodmansee and Wallach this volume). Nutrient availability declines through succession (fig. 2A). It should be noted that many fire effects upon nutrient availability are indirect: (1) accelerating decomposition (Stark 1973; but see Stark 1977; Grigal and McColl 1977), (2) speeding ammonification and/or nitrification (Christensen 1973), (3) altering pH which may either increase or decrease availability

of phosphate, nitrogen, and various cations depending upon initial conditions and the nature of the fire-induced pH change (Daubenmire 1968; Viro 1974), and (4) decreasing soil cation exchange capacity through destruction of organic matter (Van Cleve unpubl.) or alteration of clay chemistry (Daubenmire 1968). These indirect effects of fire upon nutrient availability may last for many years and over time may be more important in explaining improved plant growth after fire than is the direct release of nutrients to soil in ash (Woodmansee and Wallach this volume). For example, in certain cases the quantity of nutrients released in ash is less than that acquired by vegetation immediately following fire (Hart and others 1932). Often an element such as nitrogen may actually decrease in availability following fire and consequently may be absorbed to a lesser extent by postfire than prefire vegetation (Christensen 1977).

At high available nutrient concentrations, plants exhibit "luxury uptake" (Epstein 1972), absorbing nutrients in excess of quantities immediately used in growth. Luxury uptake may be important in the first days or weeks following fire, although this has not been examined. However, most of the plant nutrient capital of a site is not acquired immediately following fire (as discussed below), suggesting that luxury uptake and subsequent storage are not important over time intervals lasting several years.

Because nutrient uptake is an active, temperature-dependent process (Epstein 1972), the higher temperatures of blackened, recently burned soils could lead to higher nutrient uptake rates, particularly in cold climates (Wein and Bliss 1973). However, through acclimation, plants compensate for changes in root temperature and would tend to maintain similar nutrient uptake rates over a variety of soil temperatures (Chapin 1974). At soil nutrient concentrations observed under most natural conditions, plant uptake increases almost linearly with increased nutrient availability. Temperature effects upon uptake in native species may be less important than concentration effects (McNaughton and others 1974; Chapin and others 1978). The main effect of temperature upon uptake in recently burned sites is probably to increase rate of nutrient release through decomposition and therefore nutrient availability rather than to increase uptake directly. In cases where fire results in increased water availability due to decreased evapotranspiration (Woodmansee and Wallach this volume), there would be more rapid nutrient diffusion to the root surface which would increase the uptake rate of most nutrients (Dunham and Nye 1976).

To the extent that fire eliminates plants, it reduces competition for nutrients among remaining individuals and thus enhances the effective nutrient availability per plant. However, fire may diminish competition only slightly in those communities where a large proportion of the species resprout or germinate from fire-resistant seeds, as in the chaparral (Christensen and Muller 1975; Keeley and Zedler 1978), grasslands and savannas (Steward and Ornes 1975; Christensen 1977), or fire-resistant forest (e.g., sequoias and longleaf pines).

Nutrient Absorption Rate

Rapid nutrient uptake by the vegetation generally extends far beyond the time the initial pulse of fire-released nutrients remains in the soil. In fact, the rate of nutrient uptake per ground area is highest at intermediate stages of succession (Vitousek and Reiners 1975) and not immediately after the fire (fig. 2B). For example, an English heath community reaches maximum rate of nutrient removal from the soil about 10 years postfire, at which time it has accumulated half its maximum steady-state nutrient capital and is approaching its fire return time (Chapman 1967; table 1). Likewise nutrients in a Cladium jamaicense (sawgrass) community accumulate most rapidly several months after fire (Steward and Ornes 1975). Rapid nutrient absorption by mid-successional postfire vegetation could result from increasing root biomass, a change in mycorrhizal infection, or increased absorption per unit root. Little information concerning these parameters is available in relation to fire, but we may draw strong inferences from other ecological studies.

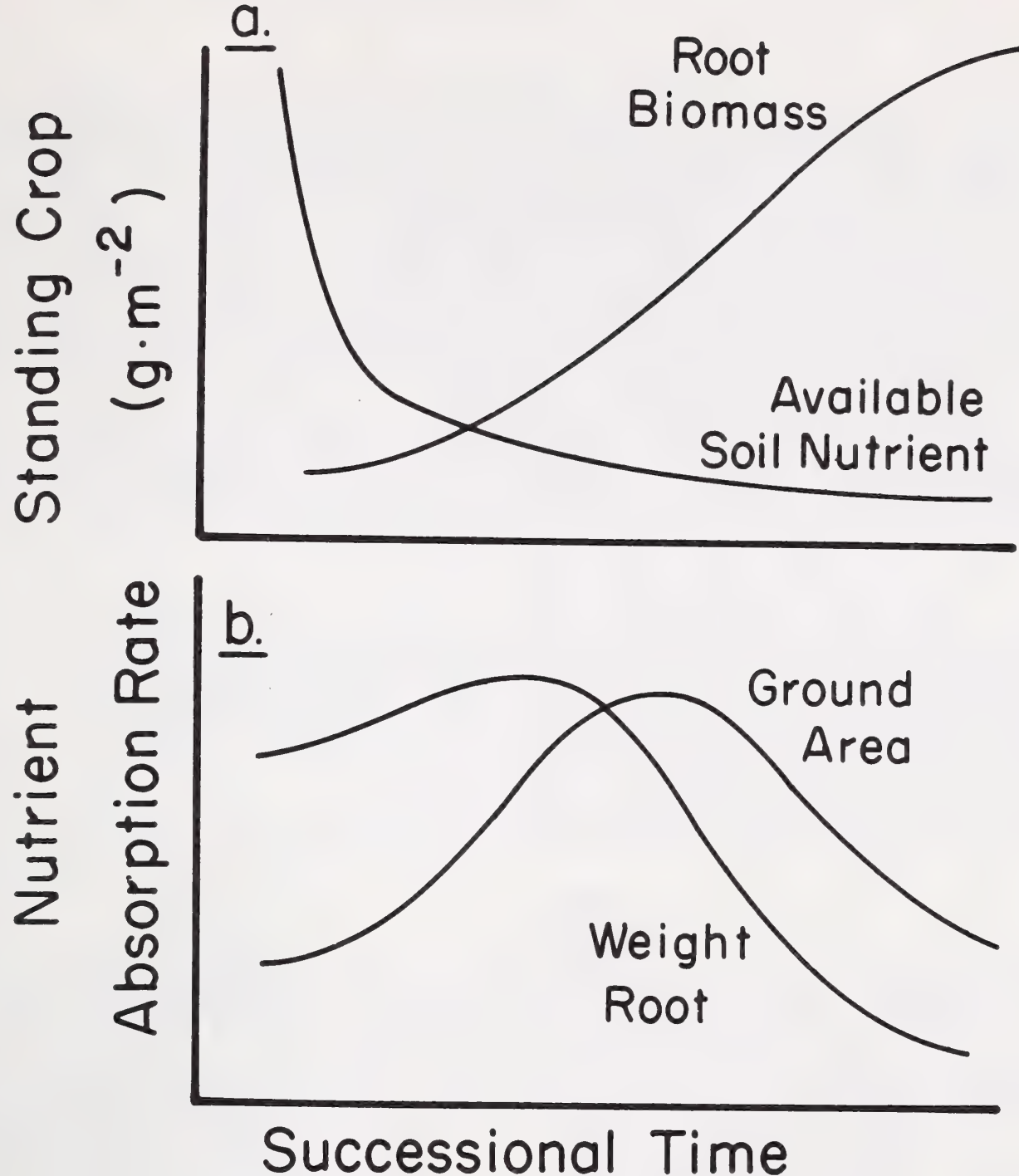


Figure 2.--Changes through succession in the various factors involved in nutrient absorption by the vegetation.

In three Alaskan taiga species phosphate absorption rates of field-collected roots were higher in early postfire communities than in more mature communities (table 2). Populus tremuloides, which is normally replaced by later successional species within 60 to 100 years after fire, has a low uptake rate 60 years postfire. Vaccinium uliginosum and Picea mariana grow relatively rapidly for the first 50 to 60 years following fire and then show slower growth and nutrient uptake rates in a mature 120-year stand. Thus, nutrient uptake rate is highest in roots from rapidly growing successional stages and declines in the mature, slow-growing 120-year stand. These observations are consistent with laboratory studies showing that plants with high relative growth rate have high nutrient absorption rates per unit root (Loneragan and Asher 1967; White 1973; Chapin unpubl.). This is to be expected because rapid growth rate entails a high nutrient requirement to support new tissue production and rapid root and leaf turnover, as described above. It is interesting that Vaccinium uliginosum and Populus tremuloides, which resprout after fire and become less prominent in late succession, show greater variation among stands of different ages than does Picea mariana, which does not survive fire but becomes dominant in late succession.

This suggests that nutrient uptake may be more plastic in these fire-surviving species than in species specialized to certain successional stages. Vaccinium and Picea, which continue rapid growth into midsuccession, have higher phosphate absorption rates at 60 years than at 5 years postfire. Nutrient availability is presumably less at 60 years than 5 years post-fire. This plant response is consistent with laboratory studies showing that plants grown under low levels of nutrient availability have high nutrient absorption rates, compensating for low soil availability (Hoagland and Broyer 1936). In summary, the data suggest that relative growth rate of plants is the main factor determining phosphate absorption rate but that, as nutrient availability declines from early to midsuccession, absorption rate increases in compensatory fashion. Finally in late succession when nutrient availability is inadequate to support a rapid growth rate, growth and phosphate absorption rates decline. The nature of cause and effect relationships between nutrient absorption and growth will be discussed in greater detail below.

TABLE 2.--Rate of phosphate absorption by excised roots of three taiga species (Populus tremuloides, Vaccinium uliginosum, and Picea mariana) collected from stands of varying ages and measured at 10° C. Mean \pm standard error, n = 4. Experimental methods are described by Chapin and Bloom (1976).

Species	Time after fire	Phosphate uptake rate
	Years	$\mu\text{g h}^{-1} \text{g}^{-1} \text{dry wt.}$
<u>Populus</u>	15	3.22 \pm 0.34
	60	1.39 \pm .19
<u>Vaccinium</u>	5	2.94 \pm .06
	60	4.00 \pm .25
	120	.93 \pm .09
<u>Picea</u>	5	2.63 \pm .22
	60	2.97 \pm .09
	120	1.70 \pm .16

In the few studies where both root biomass and soil nutrient concentrations have been examined after fire, increased nutrient uptake rates per unit root in early post-fire successional plants have been implicated (Mes 1958; Christensen 1977).

Mycorrhizal associations are extremely important in determining nutrient uptake rates by plants, although there has been little work on changes in mycorrhizal function through postfire succession. The pronounced change in fungal species composition and biomass after fire and through succession (Cooke and Laurence 1959; Latter and others 1967; Speir 1977) certainly suggest a change in mycorrhizal activity. Slash burning reduces degree of mycorrhizal infection of Douglas-fir seedlings for at least 2 years postburn (Wright and Tarrant 1958). In general, mycorrhizal associations are most strongly developed in low-nutrient habitats and should be particularly important in mid- to late succession after fire. The long-lived nature of roots in late successional species would also enhance degree of mycorrhizal infection.

Nutrients are most available to plants in the first weeks or months following fire, so there should be strong selection for roots of resprouting species to be physiologically active at this time. However, laboratory defoliation experiments indicate that roots cease to respire and to absorb nutrients immediately following defoliation and do not begin to absorb nutrients again until after leaf regrowth begins and leaves achieve a positive carbon balance (Oswalt and others 1959; Davidson and Milthorpe 1966). In the case of shrubs defoliated by fire, this time interval could last several months during which time nutrients might leach from the system. If, as is likely, depletion of carbohydrate reserves to support leaf regrowth is the cause of reduced nutrient uptake in defoliated laboratory plants, uptake by resprouting species is unlikely to be adversely affected by fire because of large carbohydrate stores. These stores could presumably support both nutrient uptake and shoot regrowth in resprouting species. Analogously, tundra graminoids, which also have large carbohydrate reserves, actually increase phosphate uptake rates following defoliation (Chapin and Slack in press).

Root Biomass

Root biomass continues to increase through succession, augmenting the nutrient-acquiring capability of the vegetation (fig. 2A) and partially offsetting the lower uptake rate that late successional roots may have. Early successional seedlings generally have low root-to-leaf ratios (Bray 1963), as is typical of plants grown under conditions of high nutrient availability (Leonard 1962; Davidson 1969). As succession proceeds, light, nutrients, and sometimes water become more limiting to growth, and plant biomass allocation patterns change accordingly. Therefore, as nutrients or water become more strongly limiting, root growth is favored, and, as light and carbohydrates limit growth, leaf production increases. Thus, canopy species increase root-to-leaf ratio through succession, although the ratio may remain low in understory species. In some cases root growth may be inhibited in mature communities by allelopathic substances in the soil (Christensen 1977). This limitation on root growth could place severe restraints on the nutrient acquiring capacity of late successional vegetation.

Resprouting species have a large increase in root-to-leaf ratio following fire because leaf mortality is greater than root mortality (Christensen 1977). If these species have sufficient belowground carbohydrate storage to support nutrient absorption, a large root biomass should be quite effective in exploiting the postfire pulse of nutrients and increased water availability. Such species may cease root production following fire, allocating reserves to shoot growth until a more nearly optimal root-to-leaf ratio is attained.

Average prefire rooting depth is species specific (Weaver 1958; Kummerow and others 1977; Flinn and Wein 1977) and is important in determining fire survival, particularly in communities characterized by extremely hot fires (e.g., chaparral) or by organic soils where a major portion of the rooting medium may actually be consumed by fires (Viereck 1973; Flinn and Wein 1977). Rooting depth also strongly influences a species' capacity to acquire nutrients and water. In the taiga the most deeply rooted species are most likely to survive and are among the most prominent components of the postfire resprouting vegetation (table 3). However, they form only a minor component of the mature black spruce community. Epilobium, for example, may be totally eliminated from the mature community. The deep-rooting habit is apparently disadvantageous in the mature community where nutrients enter the system largely from above in litter and throughfall, and where permafrost and low temperature limit exploitation of deeper horizons. There is likely an upper limit to the fire return time through which these species can survive vegetatively. A second group of shrubs (e.g., Ledum and Vaccinium uliginosum) is rooted in the organic horizon where most nutrients are recycled. This group remains an important component of the understory through succession and survives in those patches of organic matter that are not totally consumed by fire (Viereck 1973), as observed elsewhere (Stark and Steele 1977; Flinn and Wein 1977). High moisture content of the organic mat and variability in fire intensity cause a great deal of heterogeneity in the amount of the organic mat consumed and therefore in shrub survival after fire. Those species that are rooted in the moss layer of the mature community (e.g., Vaccinium vitis-idaea) have first access to nutrients recycled in the mature community and become more prominent as succession progresses from immature black spruce to muskeg, but are totally eliminated by fire. Thus, the deep-rooting habitat that promotes fire survival becomes increasingly disadvantageous as succession progresses, and shallow-rooted species that grow in the upper soil horizons where nutrient input is greatest are favored. Deep roots are most adaptive under a high frequency, high intensity fire regime. As fire intensity declines, the number of patches of unburned soil or soil exposed only to sublethal temperatures increases, and more species rooted in the upper soil layers survive (Viereck 1973; Stark and Steele 1977). These species successfully acquire nutrients throughout the fire cycle. From these comparisons it is apparent that resprouting and nonresprouting species are two ends of a continuum and not two distinct groups, as also noted by Flinn and Wein (1977) and Keeley and Zedler (1978).

TABLE 3.--Rooting horizon, relative abundance in the mature community and fire survival of species from a black spruce forest of central Alaska

Species	Root horizon	Prominence in mature community	Fire survival
<u>Epilobium angustifolium</u>	Mineral soil	Low	High
<u>Calamagrostis canadensis</u>	Mineral soil	Low	High
<u>Rosa acicularis</u>	Mineral soil	Low	High
<u>Vaccinium uliginosum</u>	Organic horizon	High	Spotty
<u>Ledum palustre</u>	Organic horizon	High	Spotty
<u>Picea mariana</u>	Organic horizon	High	Low
<u>Vaccinium vitis-idaea</u>	Moss layer	High	Low
Feather mosses	Moss layer	High	Low

As in the taiga, chaparral species generally differ in rooting depth, resprouting species being more deeply rooted than species that become established after fire (Hellmers and others 1955; Hoffman and Kummerow 1978), although shallow soil may diminish the degree of root niche specialization (Kummerow and others 1977). Again, the deeper rooting habit associated with fire survival may be disadvantageous in later successional stages. Even the deep-rooted resprouting chaparral species have abundant shallow lateral roots in mature stands (Hellmers and others 1955; Kummerow and others 1977).

NUTRIENT UTILIZATION

Plant nutrient status and use changes considerably through postfire succession. Resprouting and early successional species generally have higher nutrient concentrations than comparable unburned vegetation (Daubenmire 1968; table 4). This in part accounts for one of the major management uses of fire, that of improving forage quality for grazing and browsing animals (DeWitt and Derby 1955; Bendell 1974; Niering this volume). High root-to-leaf ratios of resprouting species and high nutrient uptake rates of early postfire successional species are generally responsible for high tissue nutrient concentrations, for reasons discussed above. In a few cases increased nutrient concentrations of postfire sprouts may be simply an artifact of a change in the age of tissue sampled (Christensen 1977). For example, the increase in nutrient concentration of Cladium jamaicense (sawgrass) leaves following burning of a longleaf pine savanna was comparable to that of plants that were simply clipped. Young leaves and stems, such as those produced after fire, typically have relatively small amounts of structural tissue and therefore on a dry weight basis have high concentrations of nutrients associated with metabolism (nitrogen, phosphorus, and potassium) and low concentrations of structurally bound elements such as calcium (Miltorpe and Moorby 1974; Chapin and others 1975). Most studies dealing with nutritional responses of plants to fire do not separate plant parts by age class so that the effect of tissue age and other more direct fire effects cannot be distinguished.

High leaf nutrient concentrations may last longer after fire than do high levels of available soil nutrients or tissue age effects (Stark and Steele 1977; MacLean and Wein 1977b; Van Cleve unpubl.). After the initial nutrient pulse from fire has been exhausted, high plant nutrient concentrations are associated with and presumably required for the rapid plant growth and active metabolism that characterize early to midsuccessional vegetation. Metabolically active leaves generally have high inorganic nutrient concentrations because they have small amounts of structural carbon, substantial quantities of nitrogen in photosynthetic enzymes (Bjorkman and others 1972), and high levels of phosphorus in membrane phospholipid and phosphorylated metabolic intermediates (Bieleski 1968; Kedrowski and Chapin 1978). Often changes in leaf nutrient concentrations of the vegetation after fire are associated with a change in species composition. For example, in New Brunswick, rapidly growing shrubs dominate the understory of Pinus banksiana stands and contain 25 to 65 percent of the aboveground plant nutrient capital. Later, shrubs are replaced by the slower growing pine with lower leaf nutrient concentrations, so that shrubs decline in importance as a nutrient sink (MacLean and Wein 1977b).

TABLE 4.--Increase in leaf nutrient concentrations of vegetation resprouting after a fire. Significance of increase is indicated by *($P < 0.05$), **($P < 0.01$), or ns (nonsignificant) where such information was provided by the authors.

Species	Increase in leaf nutrient concentration (% increase)				Time after fire Months	Ref. ^{1/}
	N	P	K	Ca		
<u>Aristida stricta</u>	194**	154**	203**	24*	2	1
<u>Aristida stricta</u>	4ns	5ns	15ns	29ns	6	1
<u>Cladium</u>						
<u>jamaicense</u>	230**	780**	273**	-22ns	1	2
<u>Cladium</u>						
<u>jamaicense</u>	11ns	7ns	-3ns	-12ns	6	2
<u>Andropogon</u>						
<u>scoparius</u>	10*	11ns	--	10ns	3	3
<u>Chrysopogon</u>						
<u>fallax</u>	28	--	--	--	6	4
	47	--	--	--	4	4
	65	--	--	--	3	4
<u>Carex bigelowii</u>	29*	38*	-13ns	0ns	12	5
<u>Eriophorum</u>						
<u>vaginatum</u>	26**	8ns	19**	9**	12	5
<u>Epilobium</u>						
<u>angustifolium</u>	--	78	143	-21	12	6
	-2ns	16ns	24ns	16*	36	7
<u>Arnica</u>						
<u>cordifolia</u>	38ns	17ns	-5ns	-11ns	36	7
<u>Vaccinium</u>						
<u>membranaceum</u>	--	14	325	-18	12	6
	4ns	-9ns	5ns	-22ns	36	7
<u>V. uliginosum</u>	28ns	21*	-41ns	0ns	12	5
<u>Spiraea</u>						
<u>betulifolia</u>	-9ns	-37*	9ns	-33*	36	5
<u>Ledum palustre</u>	37**	38**	35*	-16ns	12	7
<u>Populus</u>						
<u>tremuloides</u>	81**	56**	71**	86**	12	8

^{1/}

- | | |
|---------------------------|--------------------------|
| 1. Christensen 1977 | 5. Wein and Bliss 1973 |
| 2. Steward and Ornes 1975 | 6. Stark 1977 |
| 3. Smith and Young 1959 | 7. Stark and Steele 1977 |
| 4. Smith 1960 | 8. James and Smith 1977 |

STORAGE

Storage of carbohydrates either belowground or in fire-resistant stems is an obvious adaptation of fire-surviving species. Ninety percent of the biomass of many graminoids is belowground and much of this is involved in storage (Dennis 1977; Clark 1977). Resprouting chaparral shrub species are noted for their large fire resistant burls (Hellmers and others 1955; Hoffman and Kummerow 1978). Redwoods, longleaf pines, and aspens have large carbohydrate reserves except during spring growth (Schier and Zasada 1973). Storage carbohydrate supports production of new leaves and presumably continued nutrient uptake until such time as new leaves are photosynthetically self-sufficient. Because available soil nitrogen concentrations are often low following fire (Christensen and Muller 1975; Christensen 1977), whereas leaf nitrogen concentrations are high, belowground nitrogen storage may also be important, although we know of no pertinent studies. The importance of storage for resprouting after fire is shown by the frequent observation that plants that are repeatedly burned at short intervals decrease in carbohydrate concentration and capacity to regrow (Tew 1970; Donart and Cook 1970; Schier and Zasada 1973). Moreover, in many species reserves are used for spring shoot production, and fire at this time depresses regrowth (Buckman 1964).

Because of the energy diversion to storage, resprouting species would be expected to have less energy to invest in growth and reproduction in late succession than would non-resprouting species. In their study of chaparral shrubs, Keeley and Keeley (1977) found no evidence of this evolutionary "cost" of storage (i.e., decreased reproductive output), suggesting that the cost is small or is averaged over a long period of time.

ADAPTIVE STRATEGIES: SUMMARY OF NUTRIENT RELATIONS

The evidence presented above clearly indicates that the various characteristics related to nutrient uptake and use are highly interdependent and change together through a fire cycle. Following fire both nutrients and light are relatively abundant and are readily absorbed by the vegetation (fig. 3). The resulting high plant nutrient status allows plants to produce leaves with high photosynthetic rates but which require a large nutrient investment per gram of leaf. Rates of photosynthesis decline with leaf age, so that to maintain high rates of photosynthesis leaves must be replaced frequently, perhaps annually. Such rapid leaf turnover is achieved at high nutrient cost because of the inherent inefficiency of nutrient retranslocation from senesced leaves. Less is known about roots, but present evidence suggests a similar pattern of high initial nutrient investment per gram of root, rapid turnover, and high nutrient uptake rates. Because of the rapid gain of both carbon and nutrients, production is rapid, and a high relative growth rate is achieved. Both high light and high nutrient availability are prerequisites for the various interrelated traits of the high turnover strategy. Because such plants tend to grow on nutrient-rich substrates and because of the high respiratory cost associated with producing and maintaining highly active tissues (Penning de Vries 1972), we suspect that in most cases carbon is more limiting to growth than nutrients (with the possible exception of nitrogen in some cases) and that the carbon cost of changes in this basic strategy is the selective criterion of prime importance. The validity of this last generalization undoubtedly varies from place to place, depending upon availability of water and of each distinct nutrient.

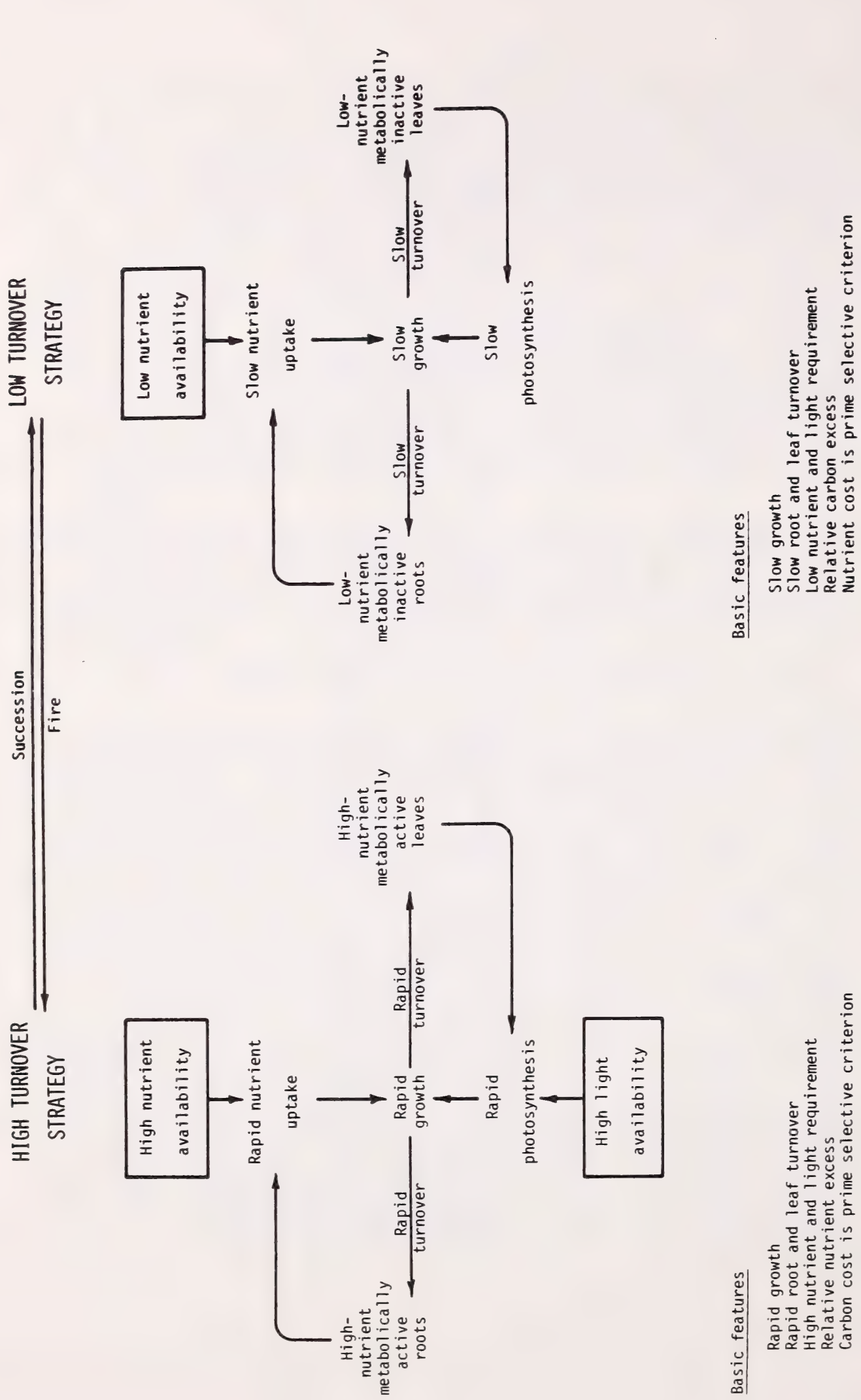


Figure 3.--Interacting characteristics of plant strategies that are adaptive under conditions of high and low resource availability and the changes in these strategies that occur as consequences of fire and succession. See text for explanation.

As succession following fire progresses, both light and available nutrients become more limiting to growth, and plants must survive the stresses of increased competition. Among canopy species where light availability remains high, the lowered nutrient status limits leaf production and turnover. It becomes advantageous to produce leaves with lower initial nutrient investment per gram of leaf, even though this leaf may entail a high carbon cost associated with structure and defense (Mooney 1972; Oriens and Solbrig 1977). Slow turnover (evergreen) leaves minimize the annual nutrient loss. Leaves with low initial nutrient investment and slow turnover have low photosynthetic rates. For analogous reasons root turnover and nutrient uptake are also slower than in early succession. Because of slow carbon and nutrient gain, relative growth rate is low in late succession. Because of inadequate nutrient supply to build new tissue, growth may be limited more by rate of tissue production than by photosynthesis. Consequently, such plants can tolerate accumulation of a large biomass and associated maintenance respiration. We suggest that, for canopy species, nutrient cost is the prime selective criterion governing variations upon this theme.

In environments where fire return time is sufficiently long to allow successional change in species composition, there is a characteristic change from species with high annual resource requirements to species with low annual resource requirements. This is typical of many successional changes (Drury and Nisbet 1973; Connell and Slatyer 1977). Growth and nutrient utilization characteristics in fire successional species may not differ greatly from those of comparable species from other successional sequences.

In contrast to species that grow over a limited range of successional stages, fire resprouting species must successfully exploit the entire range of conditions. The major adaptation that makes this possible is a high degree of phenotypic plasticity in all growth-related characteristics. Thus, as the community matures, fire-resprouting species alter nutrient uptake rates, tissue nutrient concentrations, growth rates, leaf turnover (in the case of evergreens and graminoids), and probably photosynthesis. This phenotypic plasticity is greater than that observed in species specialized to exploit the conditions of a single successional stage as documented earlier in this paper. This is consistent with Bradshaw's (1965) observation that phenotypic plasticity is selected for when the time scale of environmental change is similar to or shorter than the lifetime of the organism. As fire frequency decreases, a larger proportion of plant species complete their life cycle within the fire cycle, and fire-resprouting becomes less prominent.

ADAPTIVE RESPONSES TO FIRE AND GRAZING

Various selective forces may have led to belowground carbohydrate storage and capacity to resprout following severe defoliation, chief among these being herbivory. The effects of fire and grazing upon the plant are similar in the following respects: (1) Both remove aboveground material, increasing the root-to-leaf ratio. Thus, the plant has decreased capacity to gain carbon and a higher root biomass to support each new or remaining leaf, i.e., the plant becomes relatively more carbon-limited. (2) Grazing and low intensity fire both remove the youngest, most nutrient-rich leaves and twigs (DeBano and Conrad 1978) and thus may stress nutrient as well as carbohydrate reserves. (3) Both may be selective in their effect upon the species in a community and alter species composition. (4) Both provide a pulse of readily available nutrients in ash or feces and urine. In resprouting species fire and grazing have both selected for effective belowground storage to support regrowth. Thus, species that have been exposed to a history of heavy grazing pressure may be "preadapted" to fire survival and vice versa. Interestingly, postfire vegetation with its high nutritional content and frequently low defense level (due to low carbohydrate status) is heavily utilized by herbivores, and communities where herbivore pressure is great tend to have high concentrations of essential oils and volatile defense compounds, increasing flammability. Thus, the selective forces of fire and herbivory are often closely associated and perhaps not coincidentally have led to a common plant response of belowground storage

and capacity to resprout. Mutch (1970) suggested that volatile oils and high flammability may be adaptive in promoting fire and nutrient release. However, this argument invokes group selection. We suggest that postfire herbivory is more likely to have been the prime evolutionary factor leading to high volatile oil content in high fire frequency areas. The importance of multiple selective forces in determining plant chemistry is emphasized by Rundel (this volume).

MANAGEMENT IMPLICATIONS

The differing effects of fire upon various types of plants (early successional, late successional, and resprouting) have strong implications for the use of fire as a management tool. Some of these considerations are outlined below.

Cutting and burning are often viewed as alternative methods of bringing a community to an earlier successional stage or of maintaining an early successional stage. These two approaches would have vastly different effects upon nutrient use by plants. Fire rapidly releases nutrients and through combustion disposes of accumulated carbon, so that nutrients not lost in smoke are returned to the site in a highly available form. From this standpoint fire acts as a rapid decomposer. If resprouting or newly germinated vegetation is present, the nutrients can be largely retained on the site. In contrast, cutting of vegetation may involve removal of some of the nutrient capital from the site as wood or forage products. The organic matter remaining on the site decomposes and gradually releases nutrients to the soil. If the slash contains much wood (high carbon/low nutrient content), invading microbes may actually withdraw and tie up nutrients from the soil and make nutrients less available to the vegetation. Litter and wood generally increase in total nitrogen in the initial stages of decomposition, withdrawing this nitrogen from the soil (Grier 1978; Woodmansee and Wallach this volume). Thus, cutting returns nutrients to the soil less rapidly than does fire. Burning favors rapidly growing species with high nutrient content and may provide highly palatable forage for wildlife. In contrast, species invading a cutover area may have lower nutrient requirements, grow more slowly, and be less palatable to wildlife than species invading a burn. Vegetation that resprouts following cutting should be capable of retaining those nutrients gradually released by decomposition of dead vegetation. Even in areas of substantial rainfall, nutrient loss may be largely prevented in such cutover sites (Fredriksen 1972), whereas if the resprouting of vegetation is prevented by herbicides, nutrient loss is substantial (Borman and others 1969). The importance of nutrient losses following fire must be considered in the context of nutrient input to the system from precipitation and weathering between successive fires.

The timing and frequency of fire is equally important in determining plant response. At the time of rapid spring growth carbohydrate reserves may be reduced, and burning at this time further stresses reserves. This may kill or decrease the vigor of species that would readily resprout at another time of year. Each species should be less sensitive to a given intensity of burning as the growing season progresses and carbohydrate reserves are renewed. Burning at time of maximum carbohydrate reserves (e.g., winter) should maximize the quantity of regrowth.

Often juvenile suckers that reprot after fire are highly protected against herbivores by various secondary chemical substances (Bryant, unpubl.). If burning occurs at a time when carbohydrate reserves are less developed, the plant may have insufficient carbon to both grow and "defend itself." Such regrowth may be of lesser quantity but of higher palatability to wildlife. The relative advantage of either burning regime clearly differs for a forester interested in protecting regrowth and a wildlife manager. Such predictions are largely hypothetical, and each species differs in tolerance to burning. However, an appreciation of plant growth and nutrient use under various fire regimes is of clear importance in fire management.

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SECTION II

INTEGRATING SUMMARY

The contributions in this section clearly show that fire has been a major evolutionary force which has molded the adaptive attributes of organisms. At the same time, it has been shown that certain traits of plants may serve multiple functions, an adaptive response to fire being only one. Thus, although resprouting of a plant subsequent to burning results in the maintenance of a site, and, hence, continued reproductive output of the resprouting individual, this trait may also serve the same function in response to drought, severe cold, or grazing. Thus, many of the traits we associate with plants occurring in fire-frequented habitats may serve multiple functions and may actually have arisen originally in response to selection by factors other than fire. However, such traits are certainly reinforced by selection in fire-prone environments.

It is demonstrable that certain fire-adaptive traits such as cone serotiny have a genetic basis and thus offer potential for breeding for features desirable for a given management scheme. A close study of the traits of species which are distributed in both fire-free and fire-prone environments should enrich our understanding of the kinds of fire-adaptive traits and of their variability.

Information on the adaptive attributes of plants in fire climates may be of use for management purposes in many ways. One of the most obvious is the use of knowledge of life history attributes as shown by the contributions of Keeley and Noble. By surveying a wide range of vegetation types, Keeley deduces various suites of plant attributes, particularly those related to reproductive mode, which characterize regions differing in their fire regime. These character suites can be used to make predictions about the fire regimes of regions where detailed fire history information is not available and, hence, can be used for evolving management strategies. Noble takes a somewhat different approach but also considers reproductive attributes, particularly those relating to dispersal, persistence, and establishment. The numbers of combination of these attributes is limited. The sequence of species found through time on any given site is related to fire frequency and the species available to that site. Thus, management schemes for the maintenance of various species combinations or sequences can be designed on the basis of certain life-history information.

Somewhat less obvious is the use of the physical, chemical, and physiological properties of plants for management purposes. It appears, though, that certain aspects of many species occurring in fire-frequented sites, such as high surface-area-to-volume ratios and high extractive contents, promote flammability. Whether such features have evolved in direct response to fire or to other selective forces in their environment is certainly debatable. However, these plus other physical and chemical features of plants have been used with a certain degree of success in predicting the spread of fire.

Fire alters both the nutrient balance and light relations of habitats. These relations change through successional time. Chapin showed how the physiological characteristics of plants are keyed to the differing light and nutrient regimes in a succession sequence. Although physical and biotic factors can initiate many habitat changes which are comparable to those initiated by fire, there are certain changes, particularly related to nutrient balance, which are uniquely fire related. Thus, the responses of plants and of ecosystems, and, hence, the possible management strategies, may differ in systems where fire is used to initiate change versus those where fuel is reduced using mechanical or biological methods.

It would appear that by combining our knowledge of the life history attributes of plants with information on their physical, chemical, and physiological attributes we should be able to understand the evolutionary origin of these features to differing fire regimes, and also more readily utilize this integrated information for management purposes.

Harold A. Mooney

SECTION III

ANALYSIS OF ECOSYSTEM PROPERTIES

The power of the ecosystem approach lies in its organization of system components and functional relationships for holistic analysis. Analysis of ecosystems can follow a variety of methods, some more formal than others, but it should be designed to identify critical components and linkages so that it may yield insight on causal relationships. Special emphasis should be placed on the identification of circular loop relationships between components which are often the keys to system control. Properly utilized, ecosystem analysis ought to be a powerful tool in understanding and predicting the behavior of ecosystems in relation to complex disturbance factors such as fire. This section is distinguished from the others in this book by its specific directive to examine fire with such a perspective.

The objective of this section is to assess the impact of fire on the structure and function of ecosystems. This objective has, however, several dimensions deserving special stress. One dimension is the circular feedback nature of biological systems mentioned above. We recognize that reciprocal negative and positive feedbacks are very pronounced between fire and ecosystem properties. It is particularly important that these be illuminated. As a well-known example, the chemical and physical characteristics of litter are at the same time a product of fire history and a determinant of fire frequency. How can we predict the conditions under which litter quality will shift from more favorable to less favorable for ignition?

That question points toward a second dimension: the change in ecosystem-fire relations along complex, environmental gradients. How and why do fire frequency, fuel accumulation, or speed of vegetational recovery vary along a moisture gradient? Comparative analysis has long been a powerful tool in science and in this section we seek to emphasize that approach.

A third dimension is time. Cause and effect have to be considered along a continuum of time scales. Impacts range from immediate effects associated with ignition itself, to near-term erosional responses, and to long-term selection for species or species attributes. Fire regimes may have even longer term influences on the terrain itself. Ecosystem analysis must be open-ended with respect to time.

In pursuing our objective, we did not attempt a recompilation of current knowledge of fire, but instead sought the identification of testable hypotheses of a most general nature, as well as recommendations for research and management. The scope of ecosystem analysis is too broad to be comprehensive within the limits of this section and only five aspects of ecosystems were explored by the contributors. These five aspects are: (1) energy flow and biomass dynamics, (2) chemical cycling, (3) geomorphological processes (4) interactions between terrestrial and aquatic ecosystems, and (5) ecosystem resilience.

The first two papers are relatively familiar but attention should be drawn to the fact that the third and fourth particularly stress the importance of spatial variation and time scale. Ecosystem ecologists are realizing anew the significance of transfer of energy, material, and information across the landscape. This attention is manifested under terms such as "pattern and process," "patch dynamics," or "spatial-temporal heterogeneity." A proper understanding of fire effects, as well as other phenomena, on the ecosystem level cannot be achieved without long term evaluations of history and landscape pattern. The conventional paradigm of a semi-isolated, homogeneous ecosystem is no longer sufficient for this and most other problem areas.

The final paper is not only an exploration of resilience, but also an inquiry into how we can most effectively analyze systems that may be fundamentally unstable, as many fire-prone ecosystems apparently are. By its consideration of spatial and temporal scaling, this last paper incorporates many of the points in the preceding two papers, and leads to some interesting considerations for the formulation of management policies with respect to fire.

William A. Reiners

CARBON BALANCE IN RELATION TO FIRE REGIMES

Jerry S. Olson

Senior Ecologist
Environmental Sciences Division
Oak Ridge National Laboratory
and
Graduate Ecology Program
University of Tennessee

ABSTRACT

A theory of ecosystem succession relates the continuum of fire frequency and intensities to mean annual carbon burning in major ecosystems of the world. Low fire frequency and release of C are contrasted with combinations of (1) low frequency, high release, (2) high frequency and release, and (3) high frequency, sometimes lowering mean C release and/or ecosystem productivity. Experience, literature, income-loss equations, matrix multiplications of probabilities, and Honolulu SCOPE workshop discussions suggest the following consequences: (1) Infrequent but drastic burns restart many stand developments and successions. (2) Frequent, intense burning regimes fundamentally modify ecosystem processes and composition (e.g., releasing $>100 \text{ g C m}^{-2} \text{ yr}^{-1}$ in some seasonally dry ecosystems). (3) Frequent burns, lowering available C per fire, may have as high, or lower, average burn per year (frequency x mean C burn per fire). Charts, tables, and a map of averaged annual C release, and multiplications by tentative area estimates now suggest that nonfossil C release by fire is at least slightly below the $5 \times 10^{15} \text{ g C yr}^{-1}$ recently released by burning of fossil fuels, as global CO_2 fluxes.

KEYWORDS: fire, ecosystems recovery, mathematical models, carbon budgets, biological productivity.

INTRODUCTION

My personal interest in fire and ecosystems ignited naturally from walks along North America's ragged prairie border. Many a crooked, spreading bur oak tree with

long arms, once sunlit, already were crowded among thickets of upright Hill's oak. ^{1/} That these latter had filled in a formerly open savanna became clear when I dug into deep black charcoal prairie soils, and occasionally watched the sporadic fires prune back the formidable fringe of hawthorn, crabapple, and wild plum. Brilliant gardens and graceful grasses of the prairie were rejuvenated by these fires, but later became suppressed as woody biomass increased perceptibly in the fire-free decades since my school days. Later walks in Minnesota, Wisconsin, and along the Dakota-Iowa border and in Oklahoma and Texas suggested that ecosystem distribution and function over the wider midcontinent also had changed very significantly since my grandparents settled in sod houses on Iowa's open prairie. Yet comparative analysis of these ecosystems' properties and rates of change is unfinished business even today (Kozlowski and Ahlgren 1974, Mooney and Conrad 1977, Kucera this volume).

This volume will not finish the analysis either. We begin by literally taking apart those variables and their derivatives which are affected in different ways in different places by fires of varying intensity (see Section 1 of this volume). But if we are someday to put the pieces back together in a coherent picture of the role of fire and other disturbances, a framework for comparative synthesis must also be constructed. One approach is evolutionary (see Section 2 of this volume). The framework I choose concerns stand dynamics, landscape and global geochemistry, and system principles (cf. Noble, Swanson, Woodmansee, Wright, Holling, and Ramakrishnan this volume).

My objective is to relate personal experiences, a sampling of data from the literature, plus additional discussion during the fire conference to a general theory covering the dynamics of carbon over a continuum of environments. First, I outline this theory qualitatively, giving several working hypotheses about change of ecosystem carbon over successive episodes of burning. Some ecosystems shift regimes over time, certain ones cycling through the whole gamut: from little or no fire impact, through increasing intensity and/or frequency of burning, and (perhaps) back to a condition of relatively little fire if the production of fuels becomes too meager to support much burning.

Second, to quantify this theory the hypotheses are related to equations for net change of carbon: the difference between rates of income and loss. It is through changing of these terms that various expressions for biological production and carbon turnover and balance, reviewed in the middle of this paper, are modified more or less drastically by fire regime.

Third, I take a step toward combining the risks of fire and the amount of carbon oxidized if and when burning does occur. Matrices of carbon transfer are expressed as conditional probabilities given that fire of a specified intensity occurs. Probabilities of redistribution of carbon among major groups of ecosystem components are discussed also for the normal transfers of prior-year carbon reserves and of new (early and late) production increments, and for the transfers which are modified by a given class of fires. This provides in principle for developing a theory of the normal buildup of fuels between fires, and of minor or major reductions of fuels if and when a fire occurs. Simulation models for each major ecosystem or its hypothetical disturbance/recovery cycle could be expressed by multiplying the ecosystem's state vector successively by the appropriate kind of matrix. Burning enters as a chance variable, controlled by climate and human factors.

^{1/} The bur and Hill's oak are Quercus macrocarpa and Q. ellipsoidalis. Prairie border understory of spiny trees in the Chicago region is typically dominated by numerous species of Crataegus, by Malus ioensis, and by Prunus americana, small thorny trees that are even more resistant to grazing than to fire.

Returning from equations to observed cases, I then summarize estimates of frequency, of probable fuel removal per fire, and hence average organic carbon released per year. Reviews on ecosystem types throughout this and other papers of the present volume can then be taken as a step toward broader geographic synthesis of the importance of fire in the global cycle of carbon. Clearly the CO_2 which is recycled to the atmosphere from burning of nonfossil as well as fossil carbon requires improved estimation and modeling, which may be aided by methods in table 1. The already observed net buildup of global CO_2 is more likely than not to warm many regions and to shift dynamic patterns of the global climate (see Baes and others 1976, 1977; Bolin 1977). This can enhance evapotranspiration and the risks of widespread drying, and of burning, in certain areas even if the changed global hydrologic cycle is accelerated and the global atmosphere becomes more moist on average!

HYPOTHESES OF INVERSE RELATION OF BIOMASS AND FIRE FREQUENCY

In most stand developments, biomass tends to increase with time. However, fire or other disturbance may cut this accumulation short. Fire regimes of increasing frequency tend to restrict maximum biomass to limits lower for some pools than those which might be attained with no fire or rare fire (Chapin and Van Cleve this volume). A continuum of frequencies and intensities exists. Table 1 previews four hypotheses I assume to apply to different parts of such a continuum in various areas of the earth.

Simplified, the theory is that maximum biomass (live and/or dead fuel) would be reached under the null hypothesis of little or no influence by fire, given that other conditioning factors are equal. A possible exception might be in case of stagnated mineral cycling in cold or wet climates (cf. Heinzelman this volume, Wright this volume). There live plant biomass (phytomass) in some Boreal forests may give way to lesser amounts in muskeg or bog, but with more dead organic mass as peat. Section 1 of this volume defined some big areas of the earth (polar, desert, some rain forest) where the null hypotheses (H_0) applies. It remains a challenge to seek and prove which additional areas (e.g., in parts of the deciduous forest) have not been significantly affected by fires. For example, in the midwestern sand dunes of the U.S. (Olson 1958) and in many other areas, the pioneer vegetation has too little fuel or continuity to sustain most fires which picnics or careless acts introduce. In another dune example, the basswood-maple succession of Cowles (1899), in protected Indiana dune pockets where microclimates are ameliorated, carbon and nitrogen accumulated over time, and general nutrient cycling improved with little or no interruption by fire (Olson 1958).

Alternatives to the null hypothesis (of nil burning) are assumed to take different form as the intensity and/or frequency of fire increases. Outside the exceptional, topographically protected pocket habitats just mentioned, many of the dune stands develop through pine and oak stages described in the references just given. In Indiana even jack pine (*Pinus banksiana*) propagates well on young dunes without requiring fire, either for cone opening or seedbed, but it disappears more promptly than white pine (*P. strobus*) on those old dunes where there are not visible signs (snags, scars, oak sprouts) of hot or repeated burning. In the grasslands, dunes, and diverse other forest and shrub conditions, I have observed essential differences in the fire/recovery relations that seem to be covered broadly by three sets of conditions even though gradations are common between them. To simplify for overview, the alternative hypotheses 1, 2, and 3 on table 1 tend to have, respectively: (1) high intensity or fuel loss but low frequency of fires, (2) high fire intensity and high carbon loss along with high fire frequency, and (3) high fire frequency but diminished carbon loss rate (with energy release or fire intensity, dependent on weather) as the level of total and available biomass carbon is reduced by burning and, perhaps, by stand or site deterioration.

TABLE 1.--Multiple working hypotheses covering a wide variety of ecosystem developments influenced by fires of varying frequency and intensity

Null Hypothesis: Low (or zero) frequency and carbon burning.

H₀: Live and dead biomass accumulate until rates of income for each compartment of the ecosystem are nearly balanced, on average, by rates of loss by consumption, decomposition, and export--or rare, mild burning which accelerates release of CO₂ without basically changing the composition, process, or average chemical balance of the ecosystem.

Alternative hypotheses involve more or less frequent and drastic burning; shifts of income, loss, and the difference between them.

Low frequency, high burn.

H₁: Infrequent fire releases C and has other drastic effects when it occurs (overshoot-crash), restarting major new cycles of development of the same stand or of a successional sequence.

High frequency and burn.

H₂: More frequent fires naturally (or by controlled burning) prevent the ecosystems from approaching the stage that would perpetuate itself in the absence of fire.

High frequency, diminishing mean burn?

H₃: Fire regimes of high frequency and/or high intensity alter ecosystem development and perhaps the site nutrient reserves for the long-term future in fundamental ways: diminishing live and/or dead C, and perhaps the burning intensity.

The first stage in enhanced fire influence is reflected in the occasional but possibly intense burning at fairly long intervals: H_1 (fig. 1a-b). Carbon balances oscillate strongly; for example, pine forests not only enhance the chance of trees catching lightning strikes, but provide the flammable fuels which remove considerable carbon, leading to stimulation of a restart of stand development by more pines or else by the oaks. In many forests around the world only close looks for fire scars and charcoal reveal evidence of burning within the stand lifetime (Ahlgren 1974). There may be little awareness, beyond specialists in fire ecology and forestry, of the considerable importance of burning in the regeneration of the original type, or the triggering of type change from one dominant or characteristic community composition to another in many classical successions (fig. 1c-e).

The next hypothesis (H_2) covers cases in which there is a development of kinds and quantities of fuel that have recurring risk of ignition sooner than the time required for stabilization of a "mature" carbon inventory and budget that are balanced between production and decay (fig. 1c). The proposed theory holds that some stands pass through regimes governed by H_0 and H_1 to H_2 . There may even be regions, e.g., with Mediterranean-type climate, described by Mooney and DiCasteri (1973) and by Mooney and Conrad (1977), where regime H_2 could dominate very early in successional history.

The third alternative to H_0 is H_3 , for cases (fig. 1d-e) in which high frequency of fire may prevent the buildup of woody fuels anywhere near the inventory that might have been possible under regime H_0 , H_1 , or even H_2 . Many grassland situations described by Kucera (this volume) and others (Daubenmire 1968, Hadley 1970, Humphrey 1974, Jackson 1965, Kelting 1957, Klutes 1972, Leigh and Noble in press, Launchbaugh 1972) epitomize this stage. In some regions such cases become the end-product of a development leading through the continuum from one or several of the preceding fire regimes. More examples and some conjectured implications of these hypotheses constitute the remainder of this paper.

A more general inference seems to cover many cases, and the variation which exists in subsets of a continuum. Local spatial variation either in the fire frequency or in the fuel actually available for burning is likely to be greater than the variability of the product: (frequency) \times (carbon burned per fire). Frequent fires with low fuel availability and hence low CO_2 release per year may give nearly the same product as lower frequency multiplied by higher average CO_2 release per fire, for a given regime of climate, biotic factors and human regime of starting or suppressing fires. This invariance in mean burning rate will prove helpful below in contrasting ecosystem types, and in obtaining regional and global estimates of carbon flux which might otherwise seem speculative indeed.

EQUATIONS OF INCOME, RESPIRATION, AND BURNING RATES OF CARBON

For a given rate of income of organic carbon by photosynthesis, a maximum level of accumulation is approached asymptotically (Olson 1963a,b, 1964). This level (fig. 1a), and also the level which is averaged over time under hypotheses H_1 , H_2 , and H_3 (in fig. 1a,c,d) will become lower as the turnover fraction or loss coefficient of live and dead fuels lost per year increases. Clearly, burning adds a pathway and a mean rate of loss in addition to that which would occur from live and dead carbon pools by consumption and decomposition. Unless the latter rates are slowed as much as the direct increase of loss rate from burning, the addition of fire losses should, therefore, lower both the maximum and average inventory of carbon.

Of course, the steady-state levels may also be modified if the biological composition of the community changes. For populations of organisms, the formal deterministic

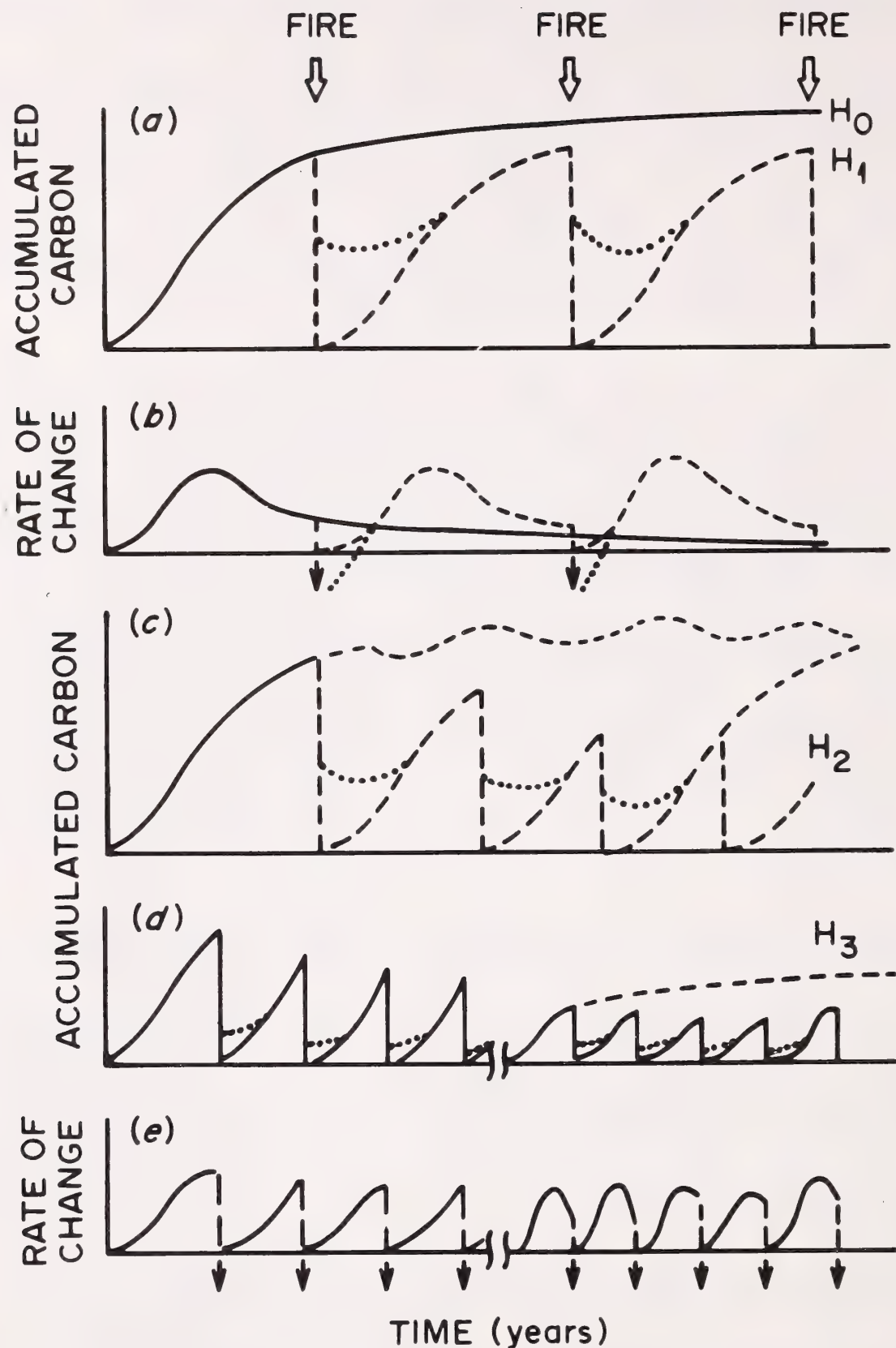


Figure 1.--Theoretical patterns of accumulated carbon in total live plant biomass (phytomass). (a) Under the null hypothesis of no burning with approach to a limiting asymptote governed by regrowth, death, and other disturbances, and the first (H_1) hypothesis involving repeated fires and regrowth similar after each one: after Tamm and others 1974. (b) Rate of change for cases in (a). (c) Variation of H_0 with oscillations around the asymptotic approach, due to minor disturbances, and a second alternative hypothesis (H_2) with increased fire frequency lowering the final and average level of biomass carbon recovery between fires. (d) Hypothesis (H_3) that still more frequent fires lower the resources and capability for regrowth, even in case the stress of fire is removed (dashed line). (e) Rate of change for (d). The dotted lines schematically reflect the realistic fact that considerable fraction of live (and/or dead) carbon is left unburned in most actual fires.

expression of net rates of change is the difference between rates of birth (plus immigration) and death (plus emigration). The use of differential equations for this purpose dates back to Verhulst (1838) and Lotka (1925). Demographic studies (Keeley, Noble this volume) still have a long way to go in resolving the shifts in community composition, from fire-susceptible to resistant or resilient species (or vice versa), theoretically by known income and loss parameters of numbers and biomass during critical phases of species life history. Successive fire events essentially provide a filter which at least can sort the relative abundance and vigor of competing species, regardless of whether or not some species enter or vanish completely according to the presence or absence of fire.

Equations for income minus loss are also crucial for treating the accumulation of dead organic materials which constitute the fuels for the next burning or for other oxidation processes. Hans Jenny and others (1949) and I (Olson 1963a) used the accumulation of litter as an example. Our discussion of loss then was oriented toward decomposition rates. But the patterns of accumulation of litter upon bare ground were taken to apply explicitly to the situation after a ground fire. Fire typically oxidizes (in part) the former accumulations of dead debris, sometimes with relatively little disturbance to the preexisting overstory stand that provides the annual income of litter.

The same kinds of income-loss equations were then applied to live biomass as a source of litter. First-order equations from constant net primary production rate and constant or variable fractional loss (by translocation plus litterfall) implied a bound on the accumulation of live plant tops (Neel and Olson 1962). This paradigm is expressed formally below; the rate equation is given on the left and the biomass equation given on the right:

$$\frac{dC_1}{dt} = p_1 - f_1 C_1 ; C_1(t) = \frac{p_1}{f_1} (1 - e^{-f_1 t}). \quad (1a,b)$$

Here p_1 is the net primary production for C_1 (carbon in compartment 1). Compartment or pool 1 represents ground vegetation only, excluding regenerating trees that can potentially reach the canopy. Current year shoots (foliage and green or hardening stems and reproductive parts) of trees are here labeled as compartment 2. After a possible lag for regeneration it undergoes a similar buildup toward a limiting value controlled by the species available and by the inherent site conditions, modified by prior soil improvement or degradation:

$$\frac{dC_2}{dt} = p_2 - f_2 C_2 ; C_2(t) = \frac{p_2}{f_2} (1 - e^{-f_2 t}). \quad (1c,d)$$

Any number of species or competing genotypes of one species could be distinguished, but for simplicity C_2 is taken below as the one which contributes woody parts and debris other than that which originates from the ground vegetation controlled by equations (1a and 1b). If the fractional loss rate f_2 is resolved in fluxes f_{ij} from part i to part j of the system, then each part j (>2) has an analogous rate and integral of change (Olson 1963b, 1964):

$$\frac{dC_j}{dt} = \sum_i f_{ij} C_i - C_j f_j ; C_j(t) = \sum_i \frac{f_{ij} C_i(t)}{f_j} (1 - e^{-f_j t}), \quad (2a,b)$$

where:

$$f_j = \sum_i f_{ji} \quad (i \neq j). \quad (2c)$$

C_1 and C_2 are not constants, but rising, ultimately asymptotic, functions like the uppermost curve of figure 1. Variables such as litter or standing dead tops which depend on live tops for their source of carbon show a lag phase while C_2 builds up. This is followed by maximum rate of increase which finally slows as C_2 and then C_j approach an asymptotic condition (Neel and Olson 1962). Root mass may tag tops, or else may be programmed genetically and by fire signals so rapid root extension precedes much top growth, e.g., in the "grass stage" of longleaf pine (*Pinus palustris*), instead of keeping root income as a constant fraction of the top (Christensen this volume).

The system of linear differential equations with constant or time-varying coefficients (depending on outside variables like climate, or else on other equations within the system) may give behavior of the same general character as the logistic or the Lotka-Volterra equations for a particular population or substance within the system, when its balance is expressed in terms of nonlinear equations. The considerable body of literature on differential and difference equations, as well as on the ecological questions which center upon determining mean and asymptotic rates, no doubt will help in implementing a wide class of ecosystem models relevant to the following discussion. Two classes of models for compartments described by rates (Eq. 2a) and changes (Eq. 2b) are controlled in part by a producer pool described either by (1c,d) or else by the logistic equation:

$$\frac{dC_2}{dt} = rC_2 - \frac{r}{h} C_2^2; C_2(t) = h/(1 - ge^{-rt}), \quad (3a,b)$$

where:

$$g = h/C_2(0) - 1. \quad (3c)$$

If these logistic formulations are chosen, the amounts of current shoots lasting through the fire and/or the regeneration (which is not modeled by the equations themselves, but by some external probability consideration) clearly influence the promptness of buildup of green parts and all the other organic materials which in turn depend on green parts.

Applied to most large regions, or to the whole biosphere, smoothing carbon budgets over annual or longer periods, these equations and mean fluxes can be construed as including losses from fire. For example, if the planetary atmosphere is taken as compartment 0 (i.e., part of the environment outside the biosphere pool), and we use left-to-right notation for subscripts, $f_{1,0}$ is the average flux of live carbon (above-ground) returned by burning. In this case, for clarity, plant respiration was already deducted, by definition, from gross primary production if we simplify the expression of inputs by using net primary production $p_1 \equiv f_{0,1}$ and $f_{0,2}$ for groundcover and tree foliage. Transfers to standing dead and litter (C_6 and C_7 in table 2), of material killed but not burned in fires, would be an additional term added to the rates of death, pruning, and litterfall which would have occurred without fire from the same class of live material. Losses to the atmospheric from C_j would include a fraction $f_{j,0f}$ of C_j directly in burning, besides the $f_{j,0r}$ returned via respiration of heterotrophic food chains--or, alternatively, traced through separate submodels for these food chains and summarized by an overall loss rate.

Next, consider those sample areas which were actually burned in a given year (compared with others in the population of sample areas which escape burning this year and burn in some other year), treating these fluxes in terms of conditional

TABLE 2.--Matrix summarizing probabilities p of transfer (or of retention) of carbon from source to destinations as a direct result of burning.

Compartment of system receiving transfer (e.g., due to fire)	Compartment of system from which transfer originates									
	Atmosphere	Producers		belowground		Con-sumer	Dead plus decomposers	(Sinks)		
	0	1	2	3	4	5	6	7	8	9
0. Atmosphere (CO ₂ , CO)		P _{1,0}	P _{2,0}	P _{3,0}		*	P _{6,0}	P _{7,0}	*	?
1. Ground vegetation		P _{1,1}								
2. Current-year shoots and fruits			P _{2,2}							
3. Coarser stems (aboveground)				P _{3,3}						
4. Belowground parts					P _{4,4}					
5. Consumers (of the aboveground)						P _{5,5}				
6. Standing (and leaning) dead		P _{1,6}	P _{2,6}	P _{3,6}	P _{4,6}	P _{5,6}	P _{6,6}			
7. Litter (with fallen logs)		P _{1,7}	P _{2,7}		P _{4,7}		P _{6,7}	P _{7,7}		
8. Soil organic matter					P _{4,8}				P _{8,8}	
9. Sinks (exports, charcoal)		P _{1,9}	P _{2,9}	P _{3,9}			P _{6,9}	P _{7,9}	*	P _{9,9}

* Transfers that are likely to have nontrivial probability for burns stronger than usual ground fire.

probabilities. Given that a fire of a given intensity class has occurred, the p 's on the diagonal summarize the probability that material in column i of table 2 remains in the same compartment in spite of the fire. Other rows in a given column with $p_{j,i}$ are those which I judge to be important quantitatively in light ground fires. One star indicates some additional fluxes which become important in passing from burns that kill consumers and char humus as well as aboveground fuel. If a short period postfire is included in the interval described by table 2 there may be a decrease in surviving belowground parts reflecting aboveground damage. The double star indicates this. It also indicates the possibility that belowground reserves which are not killed can lead to sprouting of ground vegetation and other tops before there is time for much new photosynthesis. Blanks in table 2 omit designations of minor flows for simplicity; some blanks may not be absolutely zero, but were small compared with the other cells in table 2 in cases reviewed by Mark Harmon and myself for the Great Smoky Mountains National Park.

COMPARATIVE PATTERNS IN TIME AND SPACE

The continuum of variation which is simplified by the four cases or hypotheses listed in table 1 is now discussed in terms of the general contrasts of buildup of live biomass carbon or available (live and/or dead) fuel which were presented diagrammatically in figure 1. The status of fire in various regional ecosystem complexes also is reviewed in this and subsequent sections as background for regional global estimates of CO_2 release averaged over time and space.

Null Hypothesis H_0 : Low Fire Frequency and Burn. Asymptotic Steady State

Live and dead biomass accumulate until rates of income for each compartment are nearly balanced, on average, by rates of consumption, decomposition, and export--and possibly by occasional mild burning which hardly changes the net balance of carbon or the composition of the trophic levels.

Solving Eq. (1a) for the idealized case of zero rate of change for a hypothetical limiting condition gives: $p_1 = f_1 C_1$. Equation (1b) approaches this limit, namely $C_1(t \rightarrow \infty) = p_1/f_1 = p_{0,1}/f_1$. Similarly, with constant primary production, and partitions of it to other parts of the system, $C_2(t \rightarrow \infty) = p_{0,2}/f_2$ and each other part would accumulate carbon to a level:

$$C_j = \frac{f_{2j}(C_2)}{f_j},$$

if it were fed directly from live tops. Some other levels may depend on the indirect path through other parts of the ecosystem network.

Several kinds of bogs (e.g., fig. 2) and swamps provide examples in which fire is involved only exceptionally if at all (e.g., after debris or peat have accumulated for centuries or millenia, and then been exposed to fire risk during a dry climatic oscillation, or after draining; cf. Wright this volume). Given constant solar energy input and net primary production which lags only briefly (as bare ground becomes covered), the hypothetical accumulations of live biomass (here Eriophorum vaginatum, above- and belowground), standing dead and aerobic peat are shown in figure 2a (Gore and Olson 1967). Alternative accumulation patterns for different depths of anaerobic peat at Moor House in the Pennine Mountains of England are shown in figure 2b. Losses of methane, CO and CO_2 could nearly balance our estimated Eriophorum input rate ($97 \text{ g m}^{-2} \text{ yr}^{-1}$) within one or two thousand years. If only half as much production actually reaches the anaerobic layer, the implied residence times would be twice

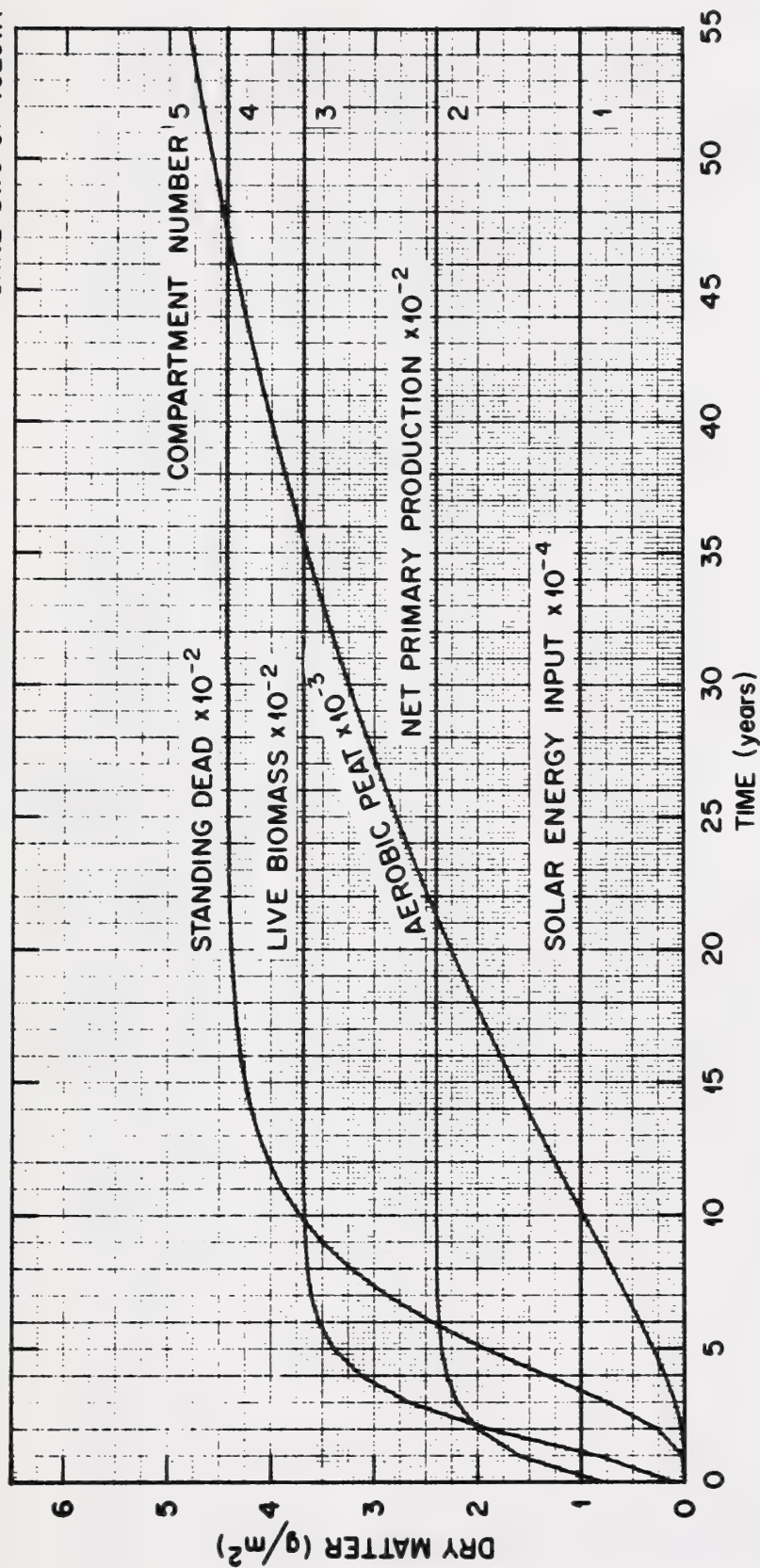


Figure 2a.--Full representation of the computer simulated behavior of five compartments of Model 1 (Eriophorum vaginatum). The model curve for aerobic peat (Compartment 5) refers only to that fraction derived from Eriophorum but illustrates the relatively slow accumulation rate of the compartment.

ANAEROBIC PEAT-COMPARTMENT 6

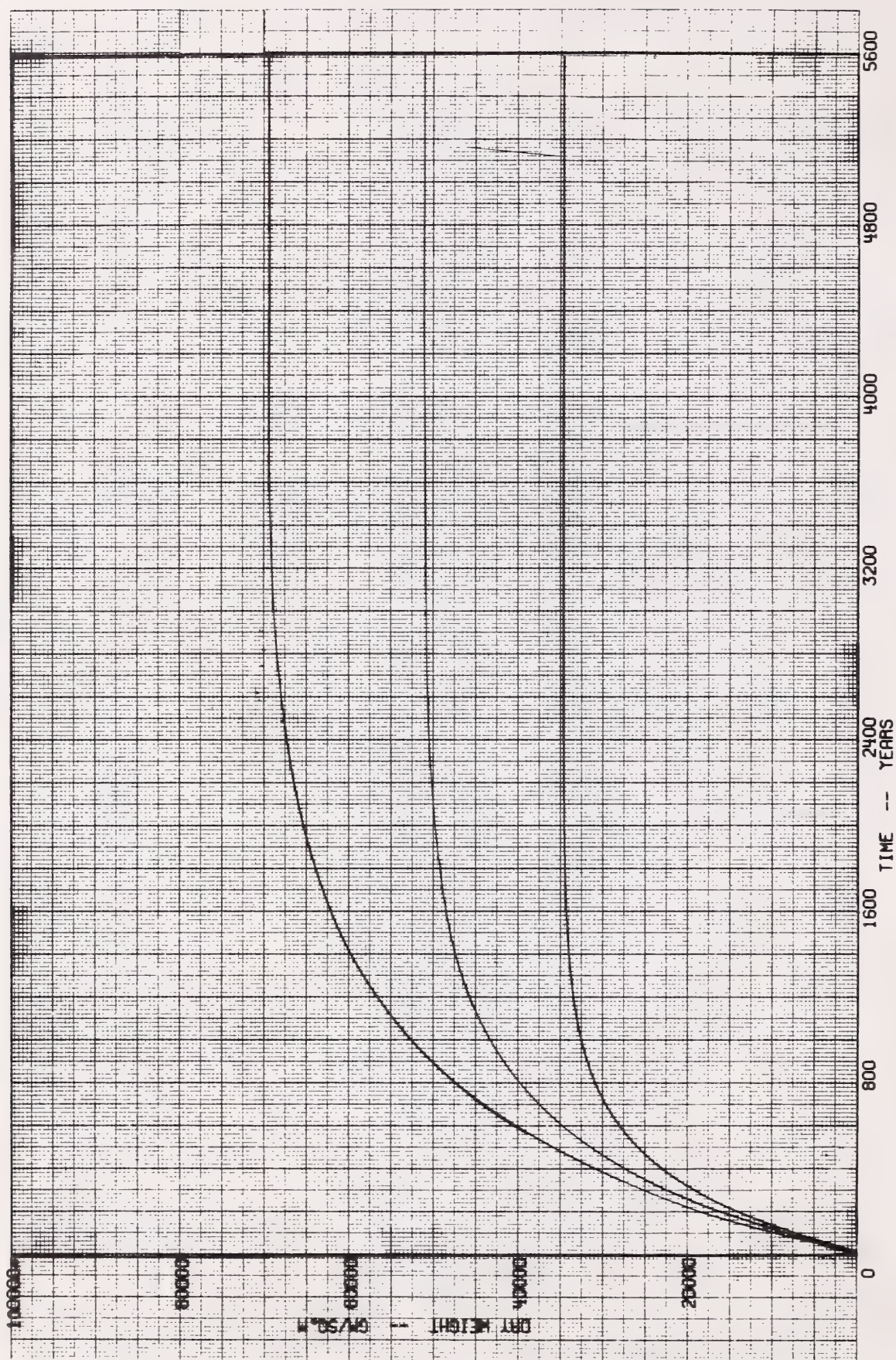


Figure 2b.--Graphic output from the computer illustrating the times required for three depths anaerobic peat to reach steady state masses. The three depths correspond to total peat depths of 60, 80, and 100 cm each including 12 cm of aerobic peat, implying a constant input of $97 \text{ g/m}^2/\text{yr}$ from the aerobic peat compartments.

as long, but still a small fraction of postglacial time: mean residence time $t = 1/f_j = 1/0.0007$ to $1/0.0014$ ($= 1,400$ to 700 years). Doubling times would be $1,000$ to 500 years ($0.693/f_j$).

For much wider bog areas, mostly of the boreal zone and parts of the tundra live carbon may have equilibrated in most areas. It is not clear whether anaerobic peat has done so. When occasional peat fires do occur, recovery may range from prompt response (H_1) to severe degradation (H_3).

Hypothesis H_1 : Low Fire Frequency High Burn. Overshoot/Crash

Infrequent but intense fire has drastic effects when it occurs, restarting major new cycles of development of the same stand or of a successional sequence.

While the idealized forest of figure 1a might approach an asymptotic level (upper curve) without fire or cutting, it seems likely that windthrow and natural diseases would lead to some episodic decreases in live carbon, followed by regrowth toward the limiting value again.

For example, with uncontrolled fires occurring after heavy fuel accumulations, observations and literature on the Boreal Forest or taiga (e.g., Heinzelman, Keeley, Smith this volume, Tamm and others 1974) indicate drastic fires of high intensity, occurring over intervals from a few decades (e.g., in midcontinental southern taiga) to several hundred years, tapering off in some of the northern taiga transitions to tundra and some maritime areas (Wright this volume). Quantitative estimates need to be approached by combining estimates of fire frequency and carbon actually burned to CO_2 per fire, as described later in this paper. For cool conifer forests of the Great Lake States, Cordilleran Mountains (Fahnestock 1976), and especially for the giant conifer forests of northwestern North America (Swanson this volume) fires probably create more CO_2 per fire, on average, from live (and dead) carbon (top row of table 2).

In terms of the remainder of table 2, hot crown fires of inflammable conifers clearly release much more than do ground fires (Smith and Henderson 1971, Brown 1975). How fires may kill essentially all the plant material ($p_{1,1} = p_{2,2} = p_{3,3} = p_{4,4} = 0$ persistence of live parts), except near moist refuges (Wright this volume). Some consumers (C_5) may flee but then return in new browse growth starts soon enough to avoid starvation. But boles and even coarse branches suddenly transfer to standing (eventually leaning and falling) dead, as represented by high probability of $p_{3,6}$; formerly standing dry snags may fall ($p_{6,7}$) as well as burn to gases ($p_{6,0}$) or to charcoal ($p_{6,9}$); or some species' belowground parts may remain living, in part preparing for resprouting (a $p_{4,2}$ flux soon after the fire). Even so, much root death provides a sudden input to soil organic matter ($p_{4,8}$).

Hypothesis H_2 : High Fire Frequency and Burn. Premature Release of Excess
Fuel Energy Lower Fuel Accumulations

More frequent fires prevent the ecosystems from approaching the stage that would perpetuate itself in the absence of fire.

Many discussions of Luke and McArthur (1977), at Mooney and Conrad's (1977) fire symposium, and in part 5 of this volume naturally emphasized prescribed burning as one management strategy to prevent highly vulnerable accumulations of either dead or living

fuels for catastrophic forest fires (Biswell 1972, 1974, 1977; Zivnуска 1977). A second, more passive strategy of merely allowing fires to burn their course--if weather conditions are not too risky for spreading beyond the designed limits--is another way of letting nature (or unplanned human-set fires) diminish the intensity of burns by tolerating greater frequency (Fahnestock 1976, Kilgore 1973, and this volume).

In table 1, the second alternative hypothesis (H_2) differs from H_1 as a matter of degree. The peaks attained for live and/or dead biomass might oscillate as a sawtooth curve as in figure 1, but tend to attain a fairly small fraction instead of a large fraction of the asymptotic level which might be approached in areas that were protected from burning. Many warm conifer-hardwood forests may reflect this intermediate fire frequency and lower mean carbon mass.

Hypothesis H_3 : High Fire Frequency, Diminished Burn. Deflected Succession.

Fire regimes of high frequency and/or intensity alter ecosystem development and perhaps site nutrient reserves which limit future carbon accumulation, species composition, and ecological dynamics.

Even under the preceding hypotheses, the opening of canopy and other effects (like mineralization of litter) by fires can stimulate the ground cover production: i.e., enhance $p_{0,1}$ after each fire is over, with or without important decreases in production of the current shoots $p_{0,2}$ and ultimately in the stems and belowground parts $p_{0,3}$ of any higher woody stratum. Hypothesis H_3 again considers a gradation, to the point where production becomes predominantly and persistently in the shrub or grass (or other herb) forms of plants. Trees may or may not persist (as isolated individuals in savannas, or grouped in parkland), but the selection discussed elsewhere in this volume would tend to shift more of the intercepted solar energy to grasses, other herbs, shrub thickets, or to more scattered sprouting woody growth than to maturing trees.

General Inferences About Carbon and Fire Regimes

Local spatial variation in fire frequency or available fuel is likely to be greater than variation in the product of two terms:

(fire frequency) x (carbon burned per fire)

Despite variations of both terms, within and between some important ecosystem groups, the resulting product offers a basis for future improvement in judging the importance of fire in the whole biosphere's carbon budget. The rest of this paper concerns this and other kinds of generalizations, and a model framework for ecosystem carbon budgets.

The next section explains how the rate equations for carbon budgets of ecosystems in general can be related to the probabilities that fires occur, and to conditional probabilities for carbon transfers (table 2) between fires, as well as during (and immediately after) them. Terrain and other site factors condition either the frequency or the intensity of the fires that do start (or spread), and the equations and probabilities for carbon balance and total nutrient regime. Landscape pattern contributes to the diversity among ecosystems which prevents successional convergence to uniform ecosystem types, and carbon budgets, in most regions.

Yet, averaging over the resulting variability within regions, there nevertheless are further patterns among regions which are discussed in all subsequent sections. In few of these regions do we find experiments giving details on the effect of fire on primary and secondary production budgets, and hence on one general issue: whether

fire makes much change in overall intake rate of carbon. But fire does make large differences in allocation to woody and nonwoody materials and in the residence time before their carbon is recycled to CO₂.

My final section before the summary uses the scattered estimates about fire frequency (or recurrence intervals) and some rather preliminary estimates of carbon loss per fire, in order to explore regularities that seem to exist in their product. When refined, the resulting estimates of carbon loss per unit area can be multiplied in turn by the areal extents of the ecosystems most affected by fire, in order to judge their importance in maintaining the global carbon budget or possibly changing it significantly.

A SIMPLE MODEL FRAMEWORK

The concept of table 2, as a bookkeeping framework for the probable carbon transfers of organic matter during a typical fire, can now be extended to a model for slower changes between fires and then to the cumulative changes over many fire-nonfire cycles. I am motivated by the fire situation of tropical savannas, specifically by the extreme example of Lamto from Lamotte (1975, 1978) and colleagues (Ceasar and Menant 1971). They have more data than are usually available, thanks to numerous French specialists and Ivory Coast staff working together in the International Biological Program. This seasonally humid Savane preforestiere is immediately adjacent to gallery forest of the Bandama River floodplain, beyond which dense evergreen forests occur on the west and east as well as south. Conversion from such forest to progressively more open savanna is believed by Lamotte (1975) to be due to burning by people, over many years, almost every January now in areas that have not been protected by other human control or by special location.

This "New Year" timing of fire simplifies presentation of the following ideas and also the mathematics of breaking up the calendar year into episodes of growth and decay before and after the burn. ^{2/} Distinctions between fires that are early, late or intermediate in the dry season are very important, as emphasized by San Jose and Medina (1975). Their experimental burn on December 28, 1968, in the Estacion Biologica de Los Llanos at Calabozo, Venezuela, provides convenient comparisons also on a calendar-year basis.

Because seasonality is so pronounced in the regions where fire is most important, the model for prefire growth may specify gross or net production as a time-varying input or forcing function. Litter fall also may be seasonal (both were modified sinusoidal functions in the early examples of Olson 1963b, 1964). Having growth and decay specified as a function of a given year's weather is especially appropriate if this can be followed by having the probability of fire itself conditioned by the availability for burning: e.g., amounts, dimensions, and dryness of the fuels (Luke and McArthur 1977).

^{2/} J. Walker (personal communication) has clarified how the burning before or after the dormant period could generally modify a matrix like that of figure 2, depending on the life cycles of species or even of fire-resistant ecotypes. For example, early fires could damage seed crops, especially in dry weather; implications for reproduction would be reflected in the model only if reproductive parts for major species groups were distinguished from other biomass components. A burn later than normal, i.e., after new vegetative growth has started, could be of serious consequence in selecting among species; a model reflecting phenology of the relevant groups could be elaborated.

One fairly simple way of treating seasonality in the probability framework already introduced with table 2 is to use matrices of the same form repeatedly. I propose several steps, with optional shortcuts. (1) The state vector $V^{(0)}$ of the variables at the beginning of year 1 (or after fire) is multiplied by one matrix $[P^{(1.1)}]$, sometimes summarized as $P^{(1.1)}$, resembling table 2 in format but instead representing growth and translocation processes (Olson and Uppuluri 1966). It gives the redistributions normally occurring up to at least the time of maximum seasonal biomass: e.g., including any resprouting of new shoots from stems or roots. (2) Another vector $W(t)$ representing new (net) primary production input prior to peak biomass is multiplied by a matrix labeled $P^{(1.2)}$ to give allocation of new increment to storage, secondary production, fresh debris, and decomposers. (3) Two vectors from these two multiplications, and a third representing additional late season production, if significant, may be separately multiplied by matrices $P^{(1.3)}$, $P^{(1.4)}$, and $P^{(1.5)}$ representing the late-season redistribution of each class of carbon. Or for simplicity, the sum of these three vectors may be multiplied instead by one matrix $P^{(1.6)}$ that gives the best combined transformation to the prefire state of the system at the end of year 1. These steps are summarized operating on different parts of the annual production budget represented by standard matrix multiplications:

$$V^{(0)} [P^{(1.1)}] = V^{(1.1)} \quad \begin{array}{l} \text{redistribution of original carbon} \\ \text{reserves until time of normal} \\ \text{maximum live biomass,} \end{array} \quad (5)$$

$$W^{(0.1)} [P^{(1.2)}] = W^{(1.2)} \quad \begin{array}{l} \text{redistribution of production} \\ \text{completed prior to time of} \\ \text{normal maximum biomass,} \end{array} \quad (6)$$

$$W^{(1.3)} = \quad \begin{array}{l} \text{additional production after} \\ \text{normal maximum live biomass,} \end{array} \quad (7)$$

$$V^{(1.1)} [P^{(1.3)}] = V^{(1.3)} \quad \begin{array}{l} \text{further redistribution of} \\ \text{prior-year reserves after} \\ \text{normal peak live biomass,} \end{array} \quad (8)$$

$$W^{(1.2)} [P^{(1.4)}] = W^{(1.4)} \quad \begin{array}{l} \text{further first-year redistri-} \\ \text{bution of previously com-} \\ \text{pleted production after time} \\ \text{of normal maximum biomass,} \end{array} \quad (9)$$

$$W^{(1.3)} [P^{(1.5)}] = W^{(1.5)} \quad \begin{array}{l} \text{redistribution of late year} \\ \text{production to increment of} \\ \text{live and dead organic mass} \\ \text{and CO}_2. \end{array} \quad (10)$$

The state of the ecosystem's vector representing live or dead carbon is the sum of the redistributed older material and the increments. These also distinguish the early and late season portions, since they may be redistributed somewhat differently by the matrices $P^{(1.4)}$ and $P^{(1.5)}$:

$$V^{(1.5)} = V^{(1.3)} + W^{(1.4)} + W^{(1.5)} \quad (11)$$

The alternative (shortcut) summary form which neglects separating the positive and negative portions of exchange in the early and late part of the year, before and after the time when maximum live biomass would normally occur, is given more briefly by:

$$\left[V^{(0)} + W^{(1.1)} + W^{(1.3)} \right] \left[P^{(1.6)} \right] = V^{(1.6)}. \quad (12)$$

In step (4a) a random number (or a fire model) determines whether fire actually occurs or not (or how severe it becomes under specified weather and control conditions). (4b) The state vector is then multiplied by the matrix of conditional probabilities like table 2, here labeled $[P^{(1.7)}]$ or $P^{(1.7)}$ to distinguish it from the other matrices:

$$V^{(1.5)} \left[P^{(1.7)} \right] = V^{(2.0)} \quad (13)$$

Several alternative matrices $P^{(1.8)}$...could even be specified to match various intensities or types of fire which, by chance, actually occurred. If no fire occurs in year 1 the state of the system after the multiplication involving $P^{(1.5)}$ or $P^{(1.6)}$ specifies the initial condition for year 2. The second year transformation matrices $P^{(2.1)}$, $P^{(2.2)}$, $P^{(2.3)}$, $P^{(2.4)}$, $P^{(2.5)}$ (or $P^{(2.6)}$) and $P^{(2.7)}$...may be similar to their counterparts for year 1 or may be time dependent.

One of the more general and interesting questions for additional modeling work is: For how long can the same numerical coefficients remain applicable even for an idealized model? For example, if the probability of burning were reduced to a fairly small fraction of 1, the same production matrices (cycled over several years) may allow a shrub savanna system like that at Lamto to regenerate the dense bush savanna and finally the wooded savanna or even the evergreen closed forest. On the other hand, in the same locale, raising the burning probability to near 1 from lower values (which allowed carryover of woody growth in some years) might be enough to drive the system from the stage of dense- to open-bush savanna, and finally through a transition to herbaceous savanna or grassland, e.g., of the *Andropogoneae* type (dominated by *Andropogon schirensis*, *Hyparrhenia* spp., etc., in West Africa). Transitions in both directions could conceivably be so drastic to represent the tangible examples of hypothesis H_3 , of deflected successions between quite different plant formations and ecosystem types. I suggest essential features distinguishing ecosystem or landscape groups are most concisely expressed by distinct patterns among the terms of their matrices during and between the fires typical of their habitats.

Further exploration may show that hypotheses H_2 and H_0 (repeated sawtooth accumulations of fire-prone vegetation of a persistent type, like chaparral; and also ecosystems with relatively minor modification by fire) can both be modeled by a set of matrices that is constant from year to year (it may vary between seasons or with weather of particular weeks within the year). Or the savanna-shrub-woodland complex may illustrate the case where the whole matrix, representing system's maintenance and transformation, changes as a result of its fire history, which in turn is conditioned by climatic history and by human habits of starting or stopping fires.

An interesting conjecture is that hypothesis H_1 (case of overshoot and crash) is even more likely than the other cases to require a shift in the fundamental pattern of production dynamics which is represented by the matrices $P^{(t,n)}$. Here t represents real change over the years and n represents a persisting shift in seasonal dynamics. Presumably this hypothesis is broad enough to encompass cycles of stand development (like in fig. 1) which are repeated with species that regenerate well by sprouting or by seed regeneration when infrequent fires do occur (Keeley this volume). Still other ecosystems have an evolutionary history and pattern of nutrient reserves and

replenishment which makes regeneration possible, following the intervening stages which we conventionally label as "fire succession," typified by different matrices and production patterns during this succession (Noble this volume).

Finally there may be cases, especially important for nature protection, where severe fire destruction, combined with other changes of site over time, make regeneration of a certain ecosystem type very improbable, even over long periods. For example, I judged this was part of the reason for absence of sugar maple forest on the old Indiana sand dunes (8,000 to 10,000 years old). Their soils also had been strongly leached of basic nutrients in black oak (Quercus velutina) ecosystems--of either the often-burned prairie savanna type or the blueberry (Vaccinium spp.) type where burning had formerly been very characteristic but less frequent (Olson 1958). This example, from Cowles' classic sand dune study areas (1899), helped me undermine an old paradigm declaring that succession tends toward convergence to or at least toward a single "climatic climax" (White 1979). It may open the way toward a new paradigm which allows probability statements to be made with some quantitative rigor about both the common and uncommon transformations which together have a part in creating the complex of landscapes we actually find so typical of various regions of the world.

FURTHER PATTERNS IN SPACE

Data from several authors and papers of this book give some examples of the contrasts of maximum or average biomass storage which can be expected from ecosystems operating under the regimes of H_0 , H_1 , H_2 , and H_3 . Chapin and Van Cleve (this volume) discuss the physiological relation of these differences: e.g., tree dominance occurring in favorable climates, over a wide range of fire frequency or intensity (their fig. 1) under my hypotheses H_0 , H_1 , and H_2 . Under poor conditions (of site or climate) for tree growth, in combination with low frequency (or better conditions and higher fire frequency), we find shrubs or even a grassy ground cover becoming widespread under the trees or eventually replacing trees when these fail to complete their life cycle. Where tree growth is inherently poor, or fire frequency very high (despite favorable conditions for trees, as in the prairie peninsula), grass-forb communities persist: H_3 .

I am concerned first with some limiting cases--on the high side. The highest biomass and carbon, live and dead (above- and belowground), occur for forests (Olson 1970a, 1974, 1975; Reichle in press). Giant conifers of the Northwestern Pacific Coast of North America attain unusually high peaks of leaf area and live and standing dead biomass (Franklin and others in press, Waring and Franklin 1979). In the climate of long, dry summers there is a relatively high probability for fires of both the ground-burning and (less frequently) the crown types. Because of the massive dimensions of old stems and their incomplete combustion, the standing dead mass is still large and undergoing decay in the early years of new forest development (typically Douglas-fir, Pseudotsuga menziesii, or lodgepole pine, Pinus contorta, after severe disturbance), when new live biomass and fresh litter from needles and small stems are still reaccumulating. For Douglas-fir logs which had fallen at the Andrews Experimental Forest near Blue River, Oreg., Cromack (personal communication) estimated minimal ages of logs of five classes of visibly progressive decay by dating seedlings of western hemlock (Tsuga heterophylla) and allowing additional time for their early establishment. Estimated annual fractional weight loss rates were 0.00736 from this method of dating and were 0.00534 using a different time estimate for log residue times by density changes. Results agree on the important point that less than 1 percent per year is released back to the atmosphere. Hence large dead logs last a long time, and seldom dry out enough to add fuel as burnable as the standing dead carbon.

Additional stands from this Pacific region, including ages up to 1,000 years for Mt. Rainier National Park, further illustrate the high values which can be accumulated for both live and dead biomass (Waring and Franklin 1979, Franklin and others in press). Such great stand ages suggest that hypothesis H_1 (overshoot-crash) is applicable to many conifer forests of the temperate and perhaps boreal zones. Stark (1973, 1977) cites other examples from Nevada and Montana, respectively, where the burning of higher frequency occurs but is usually limited to the reduction of underbrush and ground debris, with relatively modest soil nutrient depletion. Sequoiadendron gigantea in the Sierra Nevada Mountains is now believed to have had long burning histories which formerly suppressed Abies and other undergrowth (Parsons 1978, Kilgore 1973, this volume). The latter has undergone a stand development of its own in the decades since forest and park administrations suppressed fires as early as possible and limited them to the smallest possible areas.

I expect that these examples and a few others (e.g., Eucalyptus regnans in southeastern Australia, Cochrane 1968, Ashton 1975, in press) and perhaps former large Eucalyptus diversifolia of southwesternmost Australia) provide the most striking contrasts. Maximum biomass occurs with plenty of time to reach asymptotic or "overshoot" levels between fires. Fairly regular "crash" of the system to rather low levels of live biomass can be expected in due course where drought is a typical part of the regional climate. One part of the probability issue concerns how long one cycle of accumulation can proceed on a given tract without the next conflagration arising from constant or (more likely) increasing risk of finally bringing the crash to pass. A second part of the probability problem concerns table 2: the expression for how much transfer of carbon (and fuel energy) will take place for a fire of the specified kind or intensity.

The example of Tamm and others (1974) (fig. 1a) suggests that the conifer forests which typify the Boreal zone likewise undergo such a cycle. We can probably use the previously summarized averages from Rodin and Bazilevich (1967), Olson's (1970b) modification of their map and IBP data from DeAngelis and others (in press) to represent the asymptotic or "overshoot" levels of biomass for northern, middle, and southern taiga. It is not so clear what estimates provide a realistic present average over stands that are in many stages of disturbance and recovery from natural and artificial disturbances. Within the Boreal Forest most of the northern taiga (with some important exceptions as in Alaska [Barney 1971]) (Wright this volume) and the eastern maritime part of middle and southern taiga have relatively sparse trees and cool or humid climate, which diminish both the frequency and intensity of burning. On the other hand, the southern taiga, in continental climate, especially the mixed conifer deciduous areas west of Lake Winnipeg (Quintillio and others 1977) and west of Lake Baikal (Olson 1977) are almost as inflammable as the conifers of non-Boreal climates, both cool (mostly snowy) or warm (with little or no lasting snow).

Further comparisons between regions, including mean carbon loss by ecosystem type, will be made after the following section reviews some more of the pertinent literature on additional regions where fire is relatively important for natural ecological relations and for policy issues, e.g., concerning the frequency of controlled burning.

ECOSYSTEM PRODUCTION BUDGETS AND INTERACTIONS

Reduction of fuel is the explicit goal of many controlled burning strategies (Biswell 1977). Pruning of lower branches by fire scorch is common, for example, in our Oak Ridge, Tenn., controlled burns in pine stands and generally throughout the "southern pine" region of the USA as well as in numerous other regions where similar pines are native or planted. Christensen (this volume) treats the whole southeast. It is still not clear how much wild (Barden and Woods 1974) or deliberate fire modifies various categories of productivity.

Also in broadleaf evergreen forest of Australia, O'Connell (personal communication) has found that crown scorch of an intense experimental prescribed burn of jarrah (Eucalyptus marginata) at Dwellingup in western Australia prevented the normal withdrawal of phosphorus and nitrogen into woody parts before leaf fall, hastened falling to thereby thicken the litter mat prior to the normal time of excision (Nov. to Feb.), but diminished both leaf production and hence litter fall during these seasons for 2 years following the fire in March 1975. Higher mean annual phosphorus values occurred in the burned site for years 1 and 2 (0.031 and 0.019 compared with 0.014 and 0.012 percent P for the control) but nitrogen increase was more temporary (0.66 and 0.39 compared with 0.36 and 0.36 percent N) and calcium change apparently not significant (0.67, 0.72, vs. 0.62, 0.69 percent Ca). Grove (personal communication) documents increases in potassium as well as phosphorus after burning jarrah. His example bears on what I believe is an important and widespread evolutionary adaptation (internal cycling of scarce limiting nutrients). Such perturbations favor understory growth beyond the obvious means of physical destruction of woody competition by burning.

Thinning by tree death sometimes occurs incidentally to controlled burns but cannot be controlled as finely as might be desired if the purpose were to keep stands with a full canopy of pine or Eucalyptus. Enlarged openings, mineral nutrients for uptake by the ground cover, and perhaps rather specific chemical controls tend to enhance primary production of the ground stratum ($p_{0,1}$) for some interval after the fire. It would take a more data-oriented review than is possible here to document these changes extensively (cf. Groves 1977). The interesting question of whether fire leaves production increased, decreased, or left essentially unchanged in quantity (though perhaps reallocated in quality of the material produced) may be answered quite differently for various facets of production.

Production of Consumers and Decomposers

A companion SCOPE Symposium volume of "Fire and the Australian Biota" and other studies from that fire-prone continent (Luke and McArthur 1977) document additional facets of burning. An ecosystem view may lead policy to decrease the frequency of controlled burning: e.g., to about 7 years. Besides the obvious impact on plants reiterated by Gill and Noble in the present volume, the less understood effects on vertebrates (Catling and Newsome in press, Handley 1969), on soil fauna (Campbell and Tanton in press), and on soil microflora (Warcup in press) need to be placed in a general context of ecosystem production. For example, Springett (1976a) compared mature jarrah (Eucalyptus marginata) forest and a pole karri (Eucalyptus diversicolor) stand which had not been burned for 40 years (115 and 350 km south of Perth) with mild burns (350 kW/m rather than a hot burn of over 600 kW/m). Litter accumulation since experimental burning (for 1 and 5 years, respectively) had not been sufficient to increase either the numbers of species, the number of individuals, or presumably the production rates of invertebrates to the levels typical of unburned forest (with a possible exception of slightly more oligochaetes on burned jarrah). Striking functional significance for litter decay and hence nutrient cycling for the ecosystem was shown between Pinus pinaster plantations without burning (31 percent mass loss vs. no measurable mass loss in the first 27 months of litter bag exposure). Severe problems of sampling statistics as well as inherent difficulties for each organism group enhance the challenge of relating the primary and secondary production and decomposition.

Springett (1976a) cites unpublished work of Malajczuk suggesting importance of a diverse and active soil fauna for the control of the widespread soil-borne fungus pathogen Phytophthora cinnamomi. The latter can devastate jarrah stands, diminishing their primary production and nutrient cycling. She also distinguishes (1967b) two issues of concern for burning policy: reduction of faunal diversity (hence of resilience?) inherent in monoculture stands, and a mismatch of the native mesofauna with the introduced (pine needle) litter substrates that seem to be eventually mineralized mainly by fungi and bacteria. However, such differences are not reflected

in any significant difference in total invertebrate biomass (3.02, 2.97, and 3.32 g m⁻²) after 18, 23, and 31 years following controlled burn of pine plantations at Gngara (40 km north of Perth).

These are isolated examples but probably have counterparts in many regions where recycling of P and N is less critical than in Australia. But the traditional reason given for why many human cultures systematically burned many kinds of vegetation was to enhance growth of plants to be gathered, or of browse for game animals. Hunters and gatherers also aided convenient movement by burning underbrush. How well the decrease of energy for the decomposer food chains is offset by increased current energy flow in easy reach of herbivores and predators is one of the open questions.

Hill (1971) reviews the general subject of alternate pathways of carbon, cycling to animals and decomposers instead of fire fuels. Lamotte (1975, 1978), Phillips (1965, 1974), Komarek (1971), and others cited in their works, indicate that most African savannas and open woodlands have unusually high transfers through all three of these pathways, especially through termite subsystems; there is still much decomposition during the periods when moisture is favorable, so the standing crops of live and dead organic materials are much lower than in most tropical closed forests (foret dense). One of the problems arising in Africa is the overgrazing by wildlife and/or domestic stock (Pratt 1967). Also elephants in East Africa may be so vigorous in destroying trees that they create standing, leaning, and fallen dead material even sooner than might have been offered as available fuels otherwise (Olindo 1971).

Homo sapiens, of course, is the omnivore omnipotent, presumably using fire for some fraction of his several million years in Africa (Stewart 1956). Wharton (1966, 1968) emphasizes the long-term effects of wild and tame cattle, e.g., in southeast Asia. Scott (1977) emphasizes the role of fire in creating and maintaining savannas of South American highlands. Sarmiento and Monasterio's (1975) holistic approach to the general problem of savannas includes a place for climate and site factors (drainage) as well as humans and grazing (Beard 1953; Blydenstein 1967, 1968; Bourliere and Hadley 1970; Budowski 1966).

Net Woody Increment

Generally the growth of herbs and shrubs (and hence most browse) increases as the canopy of larger woody plants admits more solar energy. As the trees lose stocking density, some photosynthetically active tissue, and possibly some roots that could aid further growth, we expect the woody increment to be curtailed at least temporarily. Yet woody as well as ground cover growth may be stimulated by the nutrient release (again temporarily, perhaps) (Stark 1973, 1977; Woodmansee this volume). But we still don't know how such gains offset the other kinds of losses in total ecosystem budgets.

Total Primary Production: Gross and Net

The last point leads naturally to others. Is groundcover production plus woody plant production significantly greater or less than that of the unburned system? In the short term, where ash elements are limiting, their faster cycling rates might be expected to enhance both gross and net primary production. We also expect that drastic or frequent burns (e.g., allowing significant nutrient loss of nitrogen, ash, or eroded humus) would make the nutrient regimes significantly lower than otherwise. We might, therefore, infer decreases in gross and net primary production for this reason alone. Yet if gross production were to recover from fire (e.g., with new foliage growth) faster than new respiring tissue accumulates, it is possible to envision an increase in:

$$P_n \equiv \text{net primary production} \equiv \text{gross production} \\ - \text{autotrophic respiration} \quad (14)$$

simply because a lower respiring biomass is being supported under hypothesis H_2 or H_3 than under H_1 or H_0 .

With the exception of a few intensively studied ecosystem projects where fire was a prime object of study (as at Lamto), much of the literature on production focuses on the fraction of produce of importance for one kind of user, usually man or ungulates, but sometimes other wildlife. Biswell (1972) graphically portrays the decrease in forage as basal areas of trees increase, or of herbage as needles increase, for grassland in open woodland or parkland of Pinus ponderosa. Studies of herbage standing crop are common for individual times often judged to be near peak biomass (Launchbaugh 1964, 1972). Forage quality and composition affect gains by herbivores (Smith and Owenby 1972). However, harvest sequences treating live and dead material separately, over many time intervals for estimating net increment, are still too few (Hulbert 1969, 1973). These are related to fire treatments in some cases, but show that generalizations about fire always stimulating production can be misleading (Kucera this volume). This outcome sometimes shows fire as a stimulus, in other times a setback, requiring months or years to heal (Launchbaugh 1964, 1972). Since effects are commonly conflicting for different species, the net shifts in biomass and seed crops or their increments between burned and control plots are frequently within the considerable range of local sampling variability (e.g., Heady 1972).

Among the most challenging problems is coping with the unknown, or at least highly variable changes in belowground parts (Dahlman 1968; Dahlman and Kucera 1969a, 1969b; Kucera and Dahlman 1968). Only with more information of this kind can we improve upon the total productivity budgets and their main components (Kucera 1967, this volume).

One reason that belowground parts are so important for ecosystem productivity budgets is the need for estimating that part of underground production which serves as input to humus, instead of respiration by plants, soil fauna, and microbes that are localized in the rhizosphere (Schlesinger 1977, 1978).

Net Ecosystem Production

Having previously noted influences on secondary and primary production (woody and total), let us distinguish short-term and long-term changes in net ecosystem production. Unless the primary production rates are severely reduced, net ecosystem production is expected to increase in the early growing seasons after fire. This follows from the decrease in amounts of substrate for heterotrophic respiration and/or the temporary decrease in consumer and decomposer rates of activity per unit of substrate, as noted in a preceding section.

Whether there is an increase or a decrease over an extended period (fig. 1), including several cycles and recovery developments, may depend on whether fire loss is omitted or not from the losses that are deducted from net primary production in the arithmetic defining net ecosystem production:

$$\begin{aligned} \text{net ecosystem production} &\equiv \text{net primary production} \\ &- \text{heterotrophic respiration} \end{aligned} \quad (15)$$
$$NEP \equiv P_n - R_h$$

The material burned, either as fuels removed from the ecosystem which produced them or by wildfires in this ecosystem, logically is included as part of the net ecosystem production. Then the rate of change of the organic carbon in the ecosystem is the difference between this NEP and the additional loss: from burning in place; or the removal of material for fuel, food, or other uses; or the natural exchanges of material across the somewhat arbitrary boundaries of the ecosystem. Also, carbon oxidized to

charcoal is essentially removed from the cycle of organic matter, even though the charcoal may remain in place as another form of solid carbon for the elemental budget of the ecosystem (table 2).

The rate of change of organic carbon can therefore be related to fire losses (F) in particular by the following variants of Eq. (2a). A summary over compartment categories 1 to 8 in table 2 (or any subdivisions of these which might be appropriate in particular studies) is:

$$\frac{dC}{dt} = \text{NEP} - F \quad (16a)$$

$$= P_g (p_{0,1} + p_{0,2}) - R_a - R_h$$

$$- \sum_i p_{i,0} C_i \text{ (burning losses to atmosphere)}$$

$$- \sum_i p_{i,9} C_i \text{ (exports)} \quad (16b)$$

Evaluating these terms quantitatively would provide an important part of the biomass and nutrient modeling framework. It would complement those models which concern the physics of fire and its geophysical impact on habitat, and those emphasizing a detailed understanding of physiological/ecological consequences on the system's species. Some examples estimating the fire carbon flux term F are discussed in the next section.

TRANSLATING MEAN FIRE FREQUENCY AND FUELS AVAILABLE FOR BURNING INTO ESTIMATES OF AVERAGE BURNING

Ideally, the ecosystem's main fuel components are multiplied by the probable burning for each (top and bottom rows in table 2) and added up to estimate gaseous and charcoal loss terms for carbon in equations 2 and 16 for "typical" fires, or preferably for a range of conditions found over space and time (fig. 3). Until this can be done systematically (cf. Mooney 1977) we fall back on general estimates of mean overall burning loss per unit area, taking advantage of the tradeoff between (high frequency x low fuel) vs. (low frequency x high fuel). The resulting estimates of average loss per unit area then need to be multiplied by an appropriate area, before summing these products to obtain an estimate of carbon flux for a region or for the world. Discussing the updated area estimates in table 3 is beyond the scope of this paper, but these will be used below, along with the mean burning rates to be discussed next.

Average Carbon Loss Per Unit Area

Based on the preceding sections, literature and discussions from SCOPE workshops, appropriate ranges of local variation among areas mapped by the same symbol on the world map (fig. 4) are given in table 3. Within this range is an admittedly subjective estimate of the mean rate, derived by reasoning explained further in this section. After the parentheses is a narrower range of uncertainty which I presently attach to those means. (The reader can make other judgments and reach different overall conclusions about my average and its reliability.) Then separately, on the far right of table 3, the mean burning rates are multiplied by the corresponding areas to identify at least the generally large and small ecosystem contributions to overall global burning of nonfossil organic carbon.

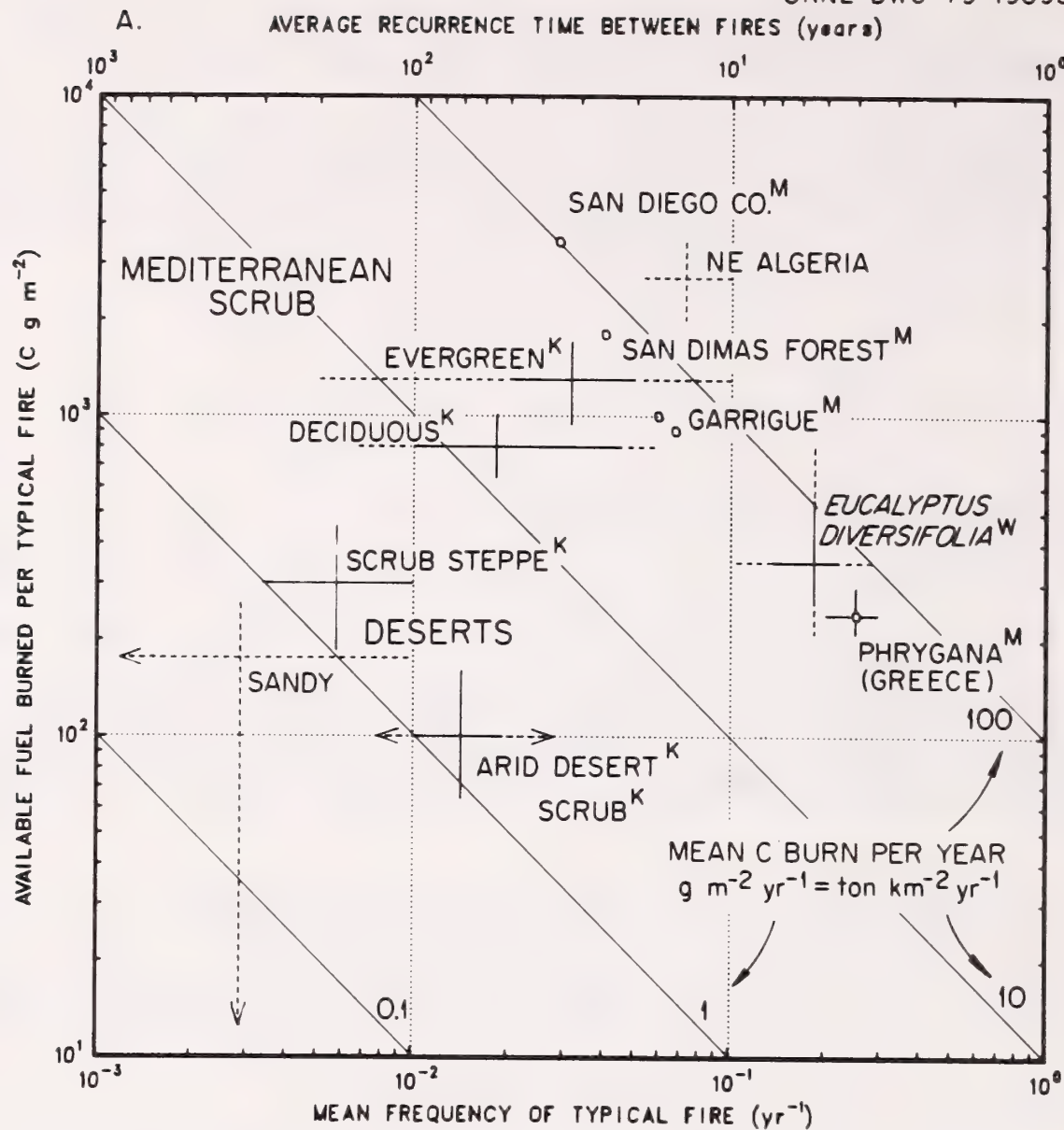
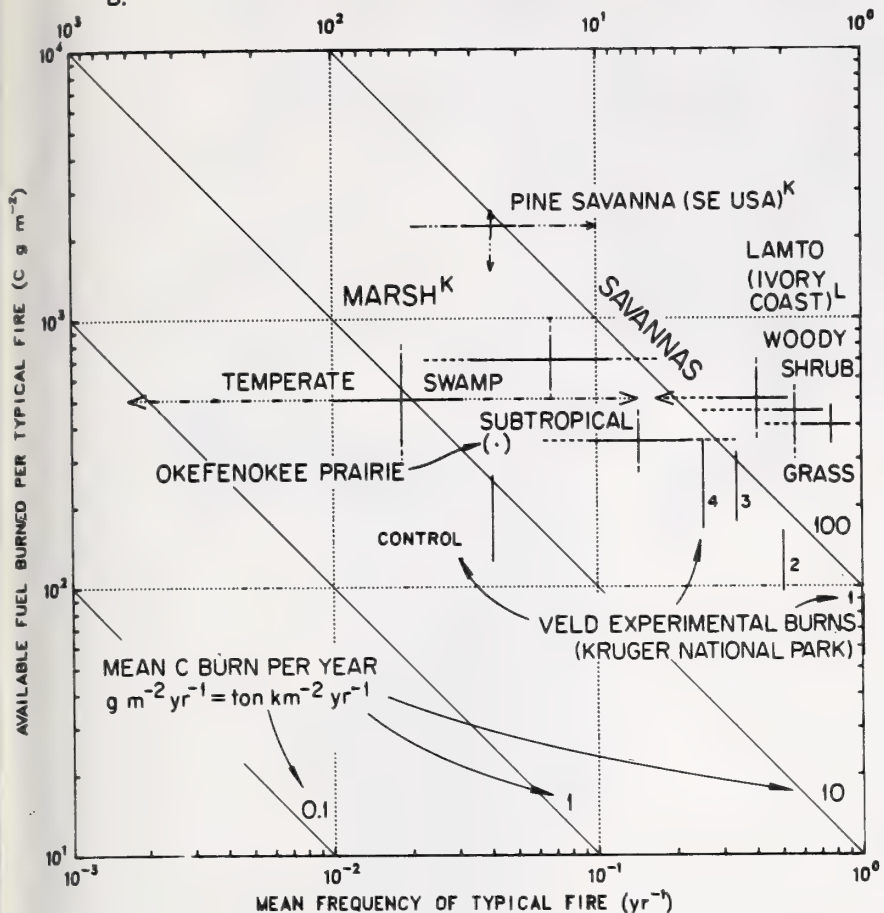
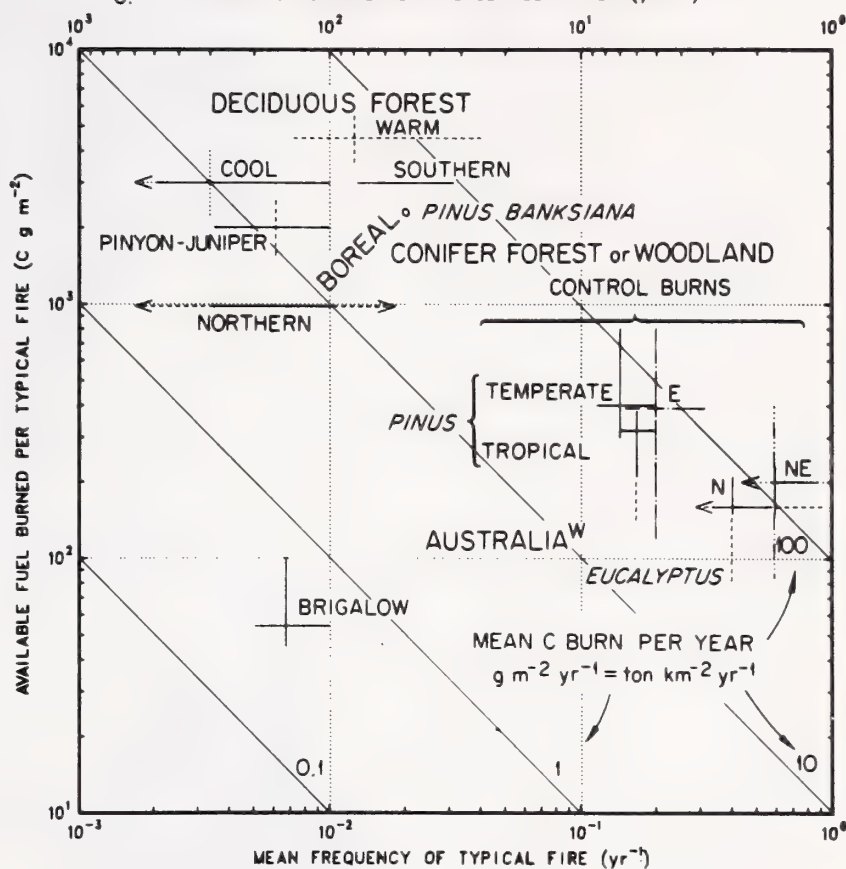


Figure 3.--Relations between mean frequency (or recurrence time) for typical fires (x axis), available fuel burned if such fires are allowed or encouraged (y axis). Mean carbon burned per year, averaging over weather conditions and fire cycles and fairly extended areas of the ecosystem type named are constant along diagonal lines, with mean burn per year given in lower area of each part of the figure. Horizontal crossed lines indicate common variability of fire interval under controlled or uncontrolled burn conditions, but some localities or estimates may range more widely as indicated by broken lines or arrows extending beyond the lifespan indicated. Vertical crossed lines indicate very preliminary estimates of carbon actually burned or available for burning in fires of the indicated frequency; the means estimated for the center of the cross are definitely subject to revision! Data sources for one or both axes are various chapters of Mooney and Conrad 1977 (M), Kucera (personal communication, Ku), tables 2, 3, and 5 of Keeley or, for *Sequoiadendron* Kilgore, this volume (K), Christensen, this volume (C), Lamotte 1978, or for Rocky Mountains, Jim Lotan and his colleagues (L), and for various parts and ecosystem types of Australia, Joseph Walker (W). A. Mediterranean, other scrub and desert types. B. Savannas, including experimental burns and protected control of Kruger National Park in South Africa, from Walker. C. Australian control burns, mostly in various *Eucalyptus* and pine plantations, contrasted with fire-resistant brigalow which burns mostly in deliberate woodland clearing operations now (Walker). Deciduous and Boreal coniferous burning increases notably from north to south. D. Wet Australian forests range from very low (mostly deliberate) burning in native rain forest to infrequent but intense burns for wet sclerophyll (Walker). Forest scrub and grasslands vary widely as indicated for burning regime, and many would have less burning where grazing or hay cutting removes the fuel.

B. AVERAGE RECURRENCE TIME BETWEEN FIRES (years)



C. AVERAGE RECURRENCE TIME BETWEEN FIRES (years)



D. AVERAGE RECURRENCE TIME BETWEEN FIRES (years)

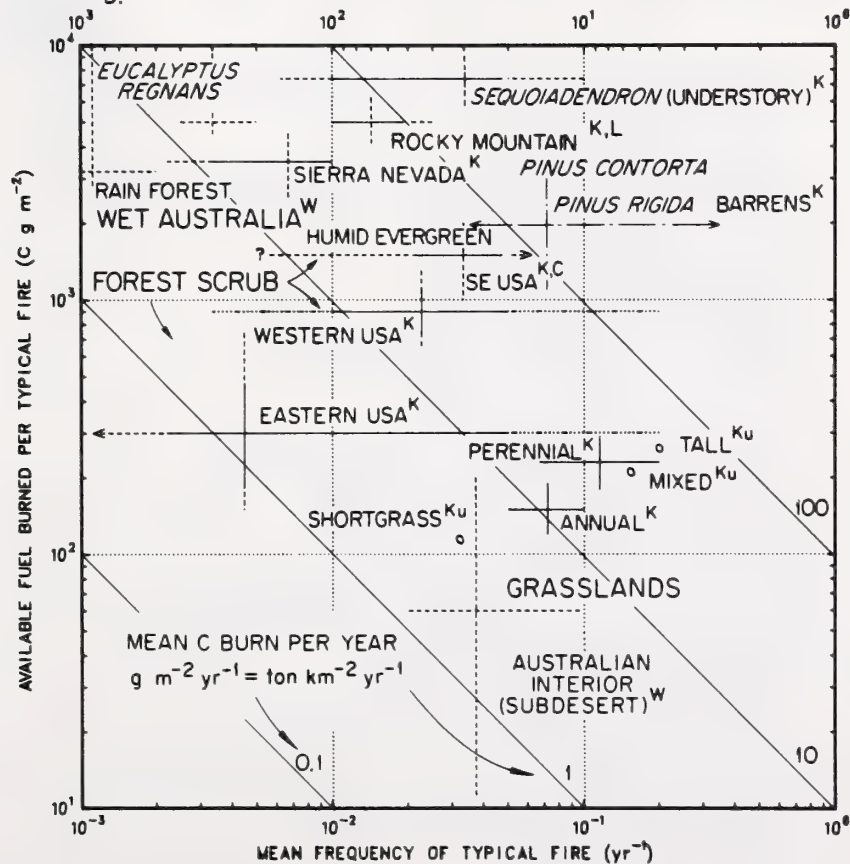
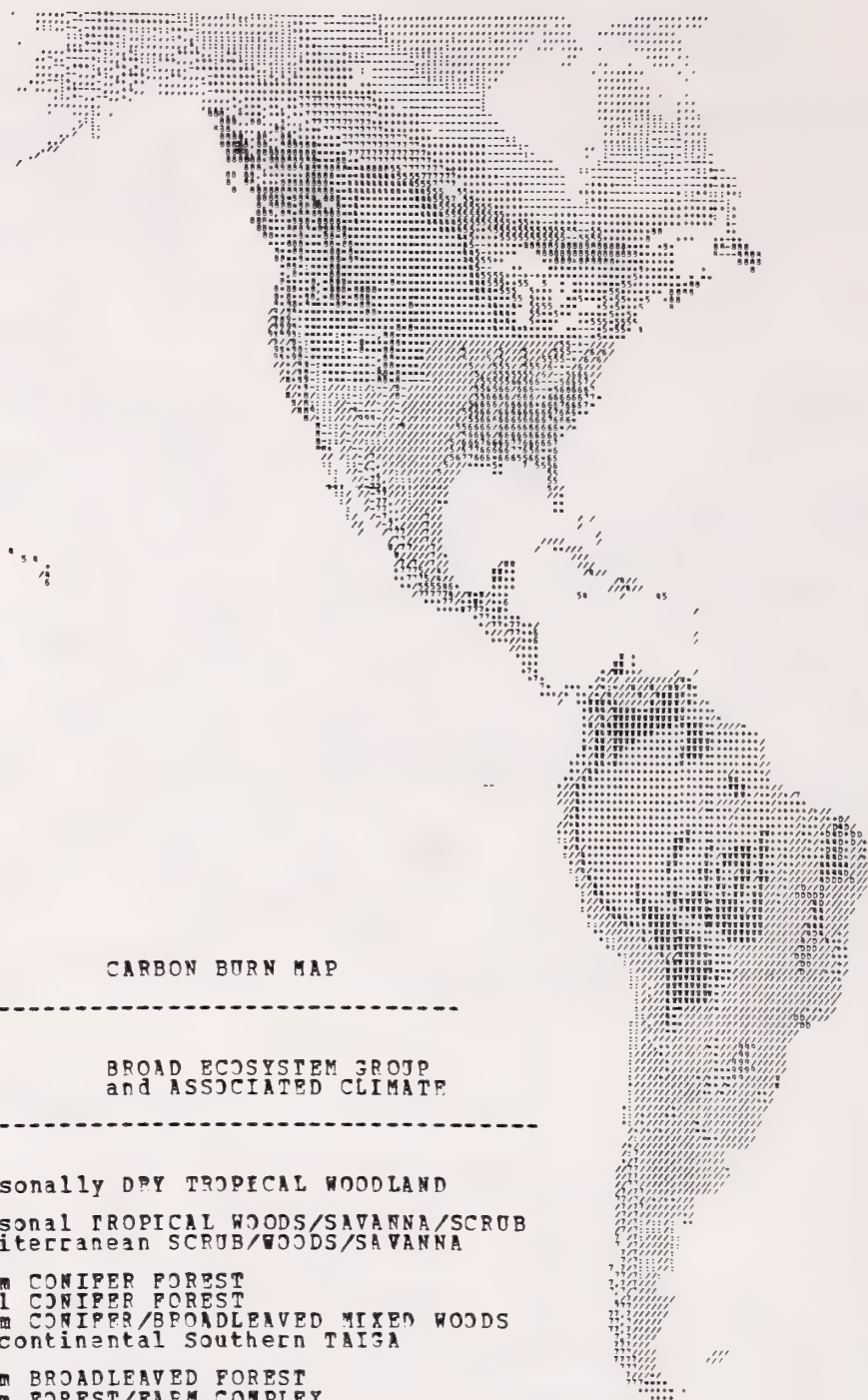


Figure 3. (continued)



CARBON BURN MAP

CODES	CARBON MEAN BURN	BROAD ECOSYSTEM GROUP and ASSOCIATED CLIMATE
D	120	Seasonally DRY TROPICAL WOODLAND
W	150	Seasonal TROPICAL WOODS/SAVANNA/SCRUB
M	100	Mediterranean SCRUB/WOODS/SAVANNA
9	90	Warm CONIFER FOREST
8	80	Cool CONIFER FOREST
7	70	Warm CONIFER/BROADLEAVED MIXED WOODS
7	70	Midcontinental Southern TAIGA
6	60	Warm BROADLEAVED FOREST
6	60	Warm FOREST/FARM COMPLEX
5	50	Cool FOREST/FARM COMPLEX
5	50	Warm SEMIARID WOODLANDS
5	50	Warm FARM, GRASS or SCRUB with WOODS
/	50	Warm FARM or GRASS/SCRUB (/TREES)
/	50	East-continental Southern TAIGA
/	40	HEATH, WOODLAND, and FARMS
4	40	Tropical MONTANE COMPLEX
4	40	Cool FARMS, GRASS or SCRUB with WOODS
/	40	Miscel. GRAZING LANDS (GRASS/SCRUB etc.)
/	40	PADDYLANDS and ASSOCIATED WOODS, TOWNS
4	40	Tropical THORN/SUCCULENT WOODS
+	30	Northern HARDWOODS/CONIFER
+	30	Middle and Eastern TAIGA
=	30	Cool GRAZING LAND (mostly GRASSLAND)
+	30	Tropical/subtropical FOREST COMPLEXES
+	30	Irrigated FARMS (dry, warm)
=	25	Irrigated FARMS (dry, cool)
=	20	Irrigated FARMS (dry, cold)
=	20	Cool FARMS or GRASS/SCRUB (/TREES)
=	20	MARSH and/or SWAMP WOODS and LITTORAL
=	20	Cold RANGELANDS
-	10	Cool DECIDUOUS FOREST
-	12	Northern or Maritime TAIGA/SUBALPINE
-	12	Sparse WOODLAND or SHRUBLAND
-	10	Low SCRUB
-	10	BOGS and BOG WOODS
:	5	SUBDESERT/DESERT SHRUBLAND, Hot
:	7	SUBDESERT/DESERT SHRUBLAND, Cool/Cold
:	3	WOODED TUNDRA
:	0.8	TUNDRA (with BOG, ROCK, POLAR DESERT)
:	0.5	SAND/SCRUB/HERBS or BARE DESERT



Figure 4.--World burning patterns and tentative rates of nonfossil organic carbon. Greater than $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (D, W, M) in seasonally dry climates with both high fire frequency and high available fuel. Approximately 40 to $90 \text{ g C m}^{-2} \text{ yr}^{-1}$ (/ , 4, 5, 6, 7, 8, 9) in agro-urban or less modified ecosystems which have either high frequency or high fuel available for burning (not necessarily both). Thirty or less $\text{g C m}^{-2} \text{ yr}^{-1}$ (-, ., ;, ;, .) burned where frequency of good burning conditions, amount or continuity of suitable fuel, or some combination of these factors reduces the product of (frequency) x (carbon oxidized per fire).

TABLE 3.--Ecosystem categories, surface area covered (km²), and estimated carbon burned for latitude limits of
66.67°N - 60.28°S

Regional ecosystem category and associated fuels and generalized climatic condition	Surface area (km ² X10 ⁶)	Local range	Estimated C ₂ burn rate (ton/km ² /yr) (mean) uncertainty	Tentative C burned totals (gton/yr) (mean) uncertainty
<u>UNESCO FORMATION CLASS I</u>				
<u>Mostly closed forest - broken by openings and lower formation types (II-V)</u>				
<u>HUMID TROPICAL/SUBTROPICAL FOREST COMPLEXES</u>				
Evergreen and/or deciduous forest with swidden fields	13.544	10-120	(30) 20-40	(0.406) 0.27 - 0.54
Tropical, subtropical montane complex	<u>1.308</u>	1-200	(40) 20-60	(.052) .026 - .078
"Humid Tropical" Subtotal	14.85			(.46)
<u>CONIFER FOREST</u>				
Cold midcontinental southern taiga	.696	30-200	(70) 40-120	(.049) .028 - .083
Cold east-continental southern taiga	.471	20-140	(40) 30-120	(.019) .013 - .057
Cold main taiga	<u>5.108</u>	10-90	(30) 20-40	(.153) .102 - .204
Mostly closed taiga sub-subtotal	6.28			(.22)
Cool conifer (winter snow and/or maritime)	2.527	10-150	(60) 40-80	(.152) .101 - .202
Warm conifer (little or no snow)	<u>.424</u>	20-200	(90) 40-80	(.038) .017 - .042
Closed Conifer Subtotal	9.23			(.41)

Table 3 continued.

TEMPERATE CLOSED BROADLEAF FOREST

Broadleaf, warm	1.216	10-200	(60)	40-80	(0.073)	0.049 - 0.097
Deciduous, cool	<u>.330</u>	5-50	(10)	8-20	<u>(.003)</u>	.002 - .007
Temperate Broadleaf Subtotal	1.55				(.08)	

MIXED CONIFER/BROADLEAF FORESTS

Cool (e.g., "Northern hardwoods-conifer")	2.070	15-90	(30)	20-40	(0.062)	0.041 - 0.083
Warm (e.g., "oak-pine," etc.)	<u>2.203</u>	40-200	(70)	50-90	<u>(.154)</u>	0.110 - 0.198
Mixed Wood Subtotal	4.27				(.22)	

FOREST/FARM COMPLEX (BROADLEAF AND/OR CONIFER)

Cool ("transition hardwoods," etc.)	.763	10-90	(50)	40-60	(0.038)	0.031 - 0.046
Warm (SE USA, etc.: deciduous and/or conifer)	<u>1.217</u>	10-150	(60)	40-80	<u>(0.073)</u>	0.049 - 0.097
Forest/Farm Subtotal	<u>1.98</u>				<u>(0.11)</u>	
CLOSED FOREST TOTAL	31.88				(1.27)	0.85 - 1.74

UNESCO FORMATION CLASS II

Mostly open woodlands, parkland or mixtures of forest with extensive low types

OPEN TAIGA (Northern or Maritime)

Open and subalpine woods, very cold	2.884	1-70	(12)	5-20	(0.035)	0.014 - 0.058
Boreal meadows and parkland, very cold	<u>.382</u>	2-50	(20)	10-30	<u>(0.007)</u>	0.004 - 0.011
Taiga Woodland/Meadow Subtotal	3.27				(0.04)	

Table 3 continued.

TROPICAL OPEN WOODS/SAVANNA COMPLEXES
(Monsoonal Droughts)

Xeromorphic woods or forest (succulent, thorn)	0.2474	20-70	(40)	30-50	(0.01)	0.997 - 0.012
Tropical woods and savanna/scrub	7.332	30-300	(150)	110-190	(1.1)	0.807 - 1.393
Dry deciduous tropical woodland	<u>3.591</u>	50-250	(120)	90-150	<u>(0.43)</u>	0.322 - 0.537
Tropical Woodland/Savanna Subtotal	11.16				(1.54)	

OTHER TEMPERATE/TROPICAL WOODLAND/SCRUB
COMPLEXES

Mediterranean woods with chaparral scrub	.7746	10-250	(100)	80-120	(0.077)	0.062 - 0.092
Semiarid woods, or tall shrubland (Australian)	.6637	15-150	(50)	30-70	(0.033)	0.02 - .046
Other dry, open woodland/rangeland	<u>1.824</u>	4-50	(12)	8-16	<u>(0.022)</u>	0.018 - .55
Other Woods/Scrub Subtotal	<u>3.27</u>				<u>(0.13)</u>	
OPEN WOODLAND TOTAL	19.70				(1.71)	1.25 - 2.18

UNESCO FORMATION CLASS IIIOther scrub - partly secondary
(Much is too local to map)

SEMIARID SCRUB/HERB/TREE RANGELANDS	12.54	0.1-80	(40)	30-50	(0.501)	.376 - 0.625
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DESERT

Sand/scrub/herbs or barren	4.797	0.01-10	(0.5)	0.2-0.8	(0.002)	0.001 - 0.004
Subdesert/shrubland, hot-warm	14.57	0.1 -20	(5)	2-8	(0.073)	0.029 - 0.117
Subdesert/shrubland, cool	<u>.081</u>	0.1 -30	(7)	4-10	<u>(0.00657)</u>	0.0003- 0.0008
Desert/Subdesert Subtotal	19.45				(0.08)	

Table 3 continued.

WOODED TUNDRA/SUBALPINE SCRUB, VERY COLD	0.7763	0.5-10	(3)	1-5	(0.0023)	0.0008-0.0004
(Extra subtotal for boreal "taiga" below 66.67° lat., including wooded tundra/subalpine: as well as forest in I, and open woodland, in II:	9.94				<u>(0.26)</u>	
SHRUBLAND/DESERT TOTAL	32.76				(0.58)	
(in addition to Mediterranean-type, old-field or other scrub associated with other woods or forest, and dwarf scrub of tundra and bogs or marshes)						
<u>UNESCO FORMATION CLASS IV</u>						
Mostly dwarf scrub and related communities						
TUNDRA WITH ROCK, ALPINE MEADOW, BOG	6.200	0.2-5	(0.8)	0.4-1.2	(.005)	.002 - .007
(Extra subtotal with wooded tundra all below 66.67°)	6.98				(0.01)	
MOSSY BOGS AND BOG WOODS, COOL-COLD	.8871	0.2-60	(10)	5-15	(.009)	.004 - .013
LOW "HEATH" AND OTHER DWARF SCRUB	<u>.1365</u>	0.1-120	(40)	30-50	<u>(.005)</u>	.001 - .007
DWARF SHRUB/TUNDRA TOTAL	7.22				(0.02)	0.01 -0.03
<u>UNESCO FORMATION CLASS V</u>						
Naturally herbaceous and/or agro-urban complexes (with variable admixtures of woody vegetation I-IV)						
FARMS (OR SAVANNAS) WITH WOODS FRINGES						
With tall grassland and woods, cool	.70	5-70	(40)	30-50	(.028)	.021 - .035
Grass/scrub/woods, warm-hot	<u>.87</u>	5-90	(50)	30-70	<u>(.043)</u>	.026 - .061
Farm with woods sub-subtotal	1.57				(.07)	

Table 3 continued.

FARM GRASS/SCRUB (TREE) COMPLEX (with towns and fringe)						
Cool farms, with settlements	4.270	1-100	(20)	10-30	(0.085)	0.043 - 0.128
Warm-hot farm, grass or settlements	<u>14.35</u>	1-200	(40)	10-70	(.574)	.143 - 1.0
Farms with towns sub-subtotals	18.62				(.66)	
(Mostly nonirrigated agro-urban subtotal)	20.19				(.73)	
PADDY LAND/SETTLEMENTS/SOME WOODS, WARM-HOT						
	2.656	1-90	(40)	20-60	(.106)	.053 - .159
IRRIGATED FARMS IN DRY REGIONS						
Warm or hot irrigated dry farmlands	1.266	10-70	(30)	20-40	(.038)	.025 - .05
Cool irrigated dry farmlands	.201	10-50	(25)	15-40	(.005)	.003 - .008
Cold irrigated dry farmland	<u>.169</u>	5-60	(20)	10-30	(.00337)	.002 - .005
Irrigated dry farm sub-subtotal	1.64				(.04)	
Argo-Urban/Fringe Subtotal	22.92				(.31)	
MARSH AND/OR SWAMP THICKET (+ WOODS)						
	1.930	0.1-80	(20)	10-30	(.039)	.019 - .05790
OTHER GRASSLAND AND FARMS						
Cool grassland	5.231	0.1-50	(30)	20-40	(.157)	.105 - .209
Warm-hot grassland	<u>8.346</u>	0.1-80	(40)	30-50	(.334)	.250 - .417
"Other Grassland" Subtotal	<u>13.579</u>				(.49)	
HERB/FARM TOTAL	40.00				(1.49)	0.69 - 2.14
NONPOLAR LAND	129.56				(4.98)	

On figure 3, intervals between typical fires are also converted to reciprocals for an expression of frequency. Burning per "typical" fire is given in units of elemental carbon (not total weight loss or CO_2 [or CO] generated). The last two numbers are multiplied to estimate average annual loss averaged over enough burning "cycles" to smooth out the statistical variations that could be expected from either factor in the product. In some cases my judgment has been made on plausible values for the average annual burning when frequency and carbon losses were not available separately, or where similar numbers (± 50 percent uncertainty) might be expected for numerous combinations of frequency and carbon release per fire in individual fires.

On figure 3, the frequency of a typical fire is given on the x axis (and fire interval is given at the top). Estimated carbon burned per fire is given on the y axis. The log-log scale implies that diagonal lines descending to the right connect products having the same average carbon release. At this stage the convenience in presenting wide ranges of frequency and/or carbon loss is important not only to indicate uncertainties, but also to suggest that whole areas of the frequency/burning domain may be typical of a region or class of ecosystem or management regimes. For example, Mediterranean-types and certain other scrub are compared on figure 3A, while figure 3B has marsh and several kinds of savannas.

Figure 3C displays wide variation among some closed forests and open woodland, for example burning in Australia ranges from very low for brigalow which has low available fuel and very low burning frequency (except in deliberate type conversion by humans) to high for pine and many Eucalyptus forests in various compass sectors of Australia (Walker personal communication). Here natural and aboriginal burning and now deliberate policies create very high frequencies and correspondingly low loads of fuel available for burning in any one fire (Walker in press, Stocker and Mott in press, Shea and others in press). Earlier I noted the contrast within Boreal forests, e.g., between higher frequency and available fuels in the continental parts of southern taiga vs. low fuel and fire frequency (rare drought years, or spots near points of human arson or accident) in northern or maritime taiga (see also Slaughter and others 1971, Rowe and Scoter 1973, Lutz 1956, Viereck 1973, Quintillo and others 1977). Deciduous forests are shown also with contrasts between cool northern hardwoods and warm areas, as were noted earlier for the southeastern USA (Ahlgren 1974, Christensen this volume).

Figure 3D has some additional, extreme forest conditions, contrasted with various prairies. Except under deliberate manipulation for clearing and temporary swidden agriculture, rain forests burn rarely (some never). In Australia, wet forests include also the "wet sclerophyll" (like Eucalyptus regnans) which burns rarely but which has very high available fuel in the dry years when fire does occur. Pinus contorta has quite wide variations among fire frequencies and loads of fuel available for burning (cf. Brown 1975, Habeck and Mutch 1973) but is believed to be higher in both for much of the Rocky Mountain region compared with the Sierra Nevada (Keeley this volume). Keeley's discussion of his several tables covers many of the estimates of most common fire frequency or recurrence intervals in figure 3, along with my solid or broken lines indicating common or possible variation, respectively, on the time axis of the diagram.

Discussion of the amounts and uncertainties of "available" or "combustible" fuel is beyond the scope of the present paper (see Walker 1979), but my preliminary estimates have been included in figure 3 in order to carry the Honolulu workshop discussions to the additional step of total burning and carbon release over extended areas. Additions and corrections are welcome!

Discussion and sample calculations start with the seasonally dry tropical woodland/savanna areas and well-documented Mediterranean-type regions of scrub and

seasonally inflammable forest. Big parts of these regions seem to have fires that are energetically intense, high in carbon release, and of variable but fairly high average frequency. Behavior commonly approximates that of hypothesis 2 (table 1, fig. 1).

Tropical Woodland/Savanna Complexes

Some of the highest annual rates of carbon release appear to be associated with vegetation having some open-grown or dwarfed tree components, along with grassy or scrubby vegetation more or less continuous between the trees and larger shrubs (Batchelder 1967).

In the tropical savannas which have several months of drought following fairly prolific and continuous spread of live and dead fuel (Komarek 1971), my highest estimates of annual carbon loss were derived, adding certain assumptions in my interpreting the IBP data of Lamotte (1975, 1978) and the numerous collaborators cited in his summaries. He refers to burning essentially every year for their research site, and this is often said to be typical around many villages, pastoral and hunting regions of the tropics. In seeking generalizations over wide areas, however, I assume that various patches are missed in different years. This seems to be confirmed by satellite observations in West Africa (Baltaxe, personal communication). In figure 3, 1 unburned year in 5 was taken for grassy savanna (with or without palm trees), 2 in 5 for shrubby or tree savanna, and 3 in 5 for woody savanna or savanna woodland, but data are required for estimates documented over regions of specified areal extent. Accumulated woody fuel, in addition to current-year herbage and litter, probably leads to more carbon burned per fire in the more woody variants of the savanna, but appreciably less per year if there were as many unburned years as I used for sample calculations in figure 3B. Where burning does occur almost yearly even higher averages might be found, but the process itself would further degrade the woody component to put an upper limit on total available fuel and on its burning, by a kind of cybernetic control (hypothesis H_3 in table 1).

Conversely, the parts of the region which still have more or less continuous but open woodland presumably include ones where annual losses by fire average considerably lower than the estimates just given, for the latter removal rates would soon change the designation to one of the more open vegetation types. A wide range of possible carbon inventories would include low figures for sparse biomass carbon due to aridity as well as due to burning. Where fuel is sparse, especially for some succulent (cactus) or thorny forest forms without continuous grass to carry the fire, appreciably lower annual burning is estimated than for grassy savanna, but the dry season nevertheless puts the range in the upper part of that for closed forests.

In trying to generalize for larger regions that would include all the savanna variants plus admixtures of xeromorphic woodland and drought-deciduous (monsoon) forest, my estimate in table 3 includes a wide range (30 to $300 \text{ g m}^{-2} \text{ yr}^{-1}$) of carbon lost from burning. I am totally open to suggestion as to whether $150 \text{ g m}^{-2} \text{ yr}^{-1}$ is an appropriate spatial average for this widespread complex of landscapes, which is mapped by W in figure 4. So far, this combination of climate and ecosystem is taken as the highest among the fire regimes which are long sustained, even though there are local places where the fuels accumulated over many prior years may lead to more intense burning until this backlog is much reduced.

The seasonally dry tropical woodlands (D on the map, mostly in south-central Africa) are inferred from frequencies of fire and available fuel to exceed $100 \text{ g m}^{-2} \text{ yr}^{-1}$ of carbon loss on average. But data are needed and there must be great variability here too, arising from cultural practices and from terrain modifying the spread of natural and artificial fires.

Somewhat higher fuel loadings and hence fire intensities, but generally lower frequencies of fire seem typical of the various regional types of chaparral, fynbos, and garrigue (di Castri and Mooney 1973) reviewed in the papers brought together by Mooney and Conrad (1977). Most of these give frequency-burning combinations that fall near (mostly below) the diagonal line representing an average of $100 \text{ g m}^{-2} \text{ yr}^{-1}$ of carbon burned. Deliberate burning by graziers and some other managers may increase the frequency enough to raise the average slightly above $100 \text{ g m}^{-2} \text{ yr}^{-1}$, but areas (like the phrygana in Greece) where repetition is at 3- to 5-year intervals apparently lower the release per fire below this number. As with savanna, aridity and overgrazing may diminish the scrub so much that burning in some localities is lower by an order of magnitude. Not only around the Mediterranean Sea but in some other areas of Mediterranean-type climate in Chile and parts of California and South Africa normal grazing and removal of logs and kindling lower the areal mean burning from the range around $100 \text{ g m}^{-2} \text{ yr}^{-1}$ (M on the map) to an average nearer perhaps $40 \text{ g m}^{-2} \text{ yr}^{-1}$ (/ on the map of fig. 4).

Other Woodlands and Forests

The wide range among localities in both their likely interval of burning and the fuels oxidized per fire (table 3, fig. 3) make it even more difficult to generalize about the various types of closed forest and open woodland distinguished in table 3 and figure 4. My oral presentation of preliminary estimates to SCOPE's Honolulu workshop and data and suggestions from its participants led this volume's editor to urge an interim synthesis for other major world ecosystem types.

CONIFER AND MIXED CLOSED FORESTS

The numbers on the map of figure 4 might first be taken only as a relative scaling of partially wooded vegetation from high (9) to low (4) importance of fire in releasing organic carbon to CO_2 or fire. To be provocative (inviting corrections wherever possible), I suggest tentatively that these numbers as averages over the ecosystem complexes of table 3 correspond approximately to annual fluxes of 90 down to about $40 \text{ g m}^{-2} \text{ yr}^{-1}$ as C. Variations within ecosystem complexes are estimated in the column under "local range" but are not mapped. Protected forests may burn less on average, even when occasional big fires that escape control are included in the average over time and space. But warm coniferous types (those with little or no snow, and fairly long seasons suitable for burning of whatever fuels have accumulated [Cooper 1960]) are provisionally estimated to approximate the upper part of this range. Cool coniferous forests, with snowy winters and/or summer temperatures moderated by maritime climate, are presently estimated to average $80 \text{ g C m}^{-2} \text{ yr}^{-1}$. Some parts (fog belt) may burn much less, but even in such climates, the giant forests of America's Pacific Northwest may have major burns at intervals of hundreds of years (Franklin and others in press). These fires create more standing and fallen dead materials which enhance the probability of a second fire (Swanson this volume). Hence long-term averages of carbon release are almost as great as for conifer forests in less snowy, more fire-prone climates.

Mixed stands and mosaics of conifer and broadleaved forest in warm (nonsnowy) climates are judged only slightly less susceptible to fire than the coniferous (non-Boreal) forests. Parts may be even more fire prone. Some include fire-resilient sprouting oaks, and other hardwoods or conifers with inflammable shrubs--as in the southeastern USA (Christensen this volume). Midcontinental sections of southern taiga, like the mixed wood with extensive fire stands of birch (Betula) and aspens (Populus) as well as jack pine (Pinus banksiana) and other conifers in central Canada

are also estimated tentatively to average near $70 \text{ g C m}^{-2} \text{ yr}^{-1}$. The areas I mapped as section 7B, and probably also that labeled 7G (central Siberian section of Southern Taiga) of Major Terrestrial Ecosystems and Environmental Gradients (Olson 1977) are assigned this high average level of mean annual carbon release rate.

The Great Lakes portion of Laurentian Southern Taiga (my section 7C) and perhaps portions of the Siberian mountain taiga-steppe complex (7H) may be only slightly less fire prone, perhaps $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ ("East-continental Southern Taiga" of table 3 and fig. 4). The same carbon release level is assigned to the cool forest/farm complex formerly occupied by the belt of transition hardwoods and white, red, and/or jack pine in the northeastern USA. However, the main belt of cool deciduous/conifer mixture, epitomized in North America by the Northern Hardwood-Conifer (Tsuga, Pinus, Picea, Larix) is believed now to average lower in general burning level, perhaps $30 \text{ g C m}^{-2} \text{ yr}^{-1}$. This level is shown by + in appropriate parts of figure 4. Less well known but also lower on a relative scale is the main belt of Middle Taiga, and probably also portions of Southern Taiga in its easterly, more maritime climate. For the widely variable burning in Northern Taiga and some very maritime sections (1 to $70 \text{ g C m}^{-2} \text{ yr}^{-1}$) it is even harder to estimate an appropriate weighted average, but slightly over 10 (say 12) $\text{g C m}^{-2} \text{ yr}^{-1}$ may even be on the high side. In brief, major conifer (and mixed wood) belts of North America and probably of the world almost span the full range of burning values of all wooded ecosystem types.

BROADLEAVED TEMPERATE

Broadleaved forests and their mixtures with openings for farms or grazing lands in warm climates (with little or no snow) are assigned the rating 6 (averaging perhaps $60 \text{ g C m}^{-2} \text{ yr}^{-1}$) for carbon release. Christensen (this volume) has already discussed some of the reasons why there is much real variability around any mean which might ultimately be found to improve upon this average estimate in the southeastern USA. On the prairie border fringe of this forest in the USA and also toward the interior fringe of semiarid woodlands in Australia according to J. Walker (1979), burning release diminishes at least to $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ and locally much lower, as in the brigalow stands and isolated woodlots that are protected from burning, except for the materials removed and used as fuel wood. In cool (snowy) climates the forest border averages still lower burning, perhaps $40 \text{ g C m}^{-2} \text{ yr}^{-1}$, except where fire is allowed or recreated in relic areas of prairie savanna.

TROPICAL LOWLAND AND HIGHLAND

While the seasonally dry tropical woodlands and related savannas were discussed earlier as outstanding examples of high burning and carbon release, there is clearly a gradation from those conditions toward the humid tropical forests and ultimately some rain forests with essentially no burning at all. Zones must someday be delineated with most of the gradations of burning probability and carbon release which have just been discussed for temperate and Boreal forests. Furthermore, some of the wettest tropical forest areas have dry seasons just long enough for local people to fell, dry, and burn at least the smaller-dimension fuels for swidden agriculture. Without attempting (fig. 4) to define the rather intricate geographic variations, I just use a + to cover these and other types which are judged to release $30 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average.

Tropical areas marked 4 include xeromorphic (thorn and/or succulent) woods like the eastern Brazilian caatinga (not the savanna and low woods caatinga areas further west). Seasonal droughts (Mueller-Dombois this volume) presumably favor burning, but limited production, heavy removals, grazing, and the succulent character of some

vegetation restrict amounts of fuel available for burning. It is not clear whether the implied loss rate of $40 \text{ g C m}^{-2} \text{ yr}^{-1}$ for this or the following type is a good average over any wide areas.

Also in the tropics, 4 is used to suggest that slightly higher average burning is expected (locally much higher) in many of the montane ecosystem complexes where farming and/or grazing have been or are currently being expanded. However, locally within the same symbol areas there may be montane cloud forests, paramo, and alpine or rock surfaces where fire is nil.

Other Ecosystem Groups

Besides closed forest and open woodlands (groups I and II in the Unesco classification of vegetation), complexes of vegetation typified by shrubs, dwarf shrubs, and grass or other herbs (groups III, IV, and V on table 3) cover even greater areas of the earth. On the map of figure 4, the location of these ecosystem types (and some of the forest and woodland groups with lower annual estimated burning) are shown by symbols other than capital letters and numbers.

Diagonal lines on figure 4 cover landscape complexes which tentatively are judged to average 40 to $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ burning over wide areas but which undoubtedly have big areas of lower burning. For one example, large areas of farming and/or settlements in warm-temperate to tropical climates may have most fires concentrated in areas near the towns and in certain crops where residues are burned outdoors, or indoors as fuels. Secondly heath or moorland vegetation includes Arctic (e.g., Aleutian) areas with practically no burning, as well as Australian types approaching the Mediterranean-type regime of high burning. Intermediate burning regimes seem more typical, with or without the deliberate shortening of fire interval and decrease in fuel availability. Some paddy regions, such as those in Japan, involve very little burning. But considerable carbon in associated woods and towns might recycle to CO_2 by more or less deliberate burning for charcoal, cooking, and heat. Warm grasslands and associated scrub are probably the most widespread and important complex in this medium-burning group.

Equal signs on figure 4 (estimated 20 to $30 \text{ g C m}^{-2} \text{ yr}^{-1}$) apply to cool or cold irrigated farmland, other cool farmland and rangeland (Komarek 1965), and perhaps marshlands and swamps (with thickets and woods) that burn infrequently, but with occasional high carbon loss (Klukas 1972). Bogs and bog woods (Moore and Bellamy 1974) and several other ecosystem groups were judged to have 10 or less $\text{g C m}^{-2} \text{ yr}^{-1}$, with big areas much lower (see the marks - : ; , and . on fig. 4 legend). Their fuller discussion is beyond the scope of this forest workshop. The modest fire contributions estimated here seem more likely to be generous than low, and they include considerable oxidation to charcoal, and small amounts to CO .

Location, Areal Extent, and Overall Amounts of CO_2 and Charcoal Sources

Figure 4 is a further step toward the global geography of fire in ecosystems, taking my estimates for ecosystem type and displaying them throughout the type's (provisional) map range. Within traditional categories, taiga has been differentiated between very low vs. high regions based on general knowledge of fire frequencies. A similar refinement within the humid tropical-subtropical forest complexes (mapped as +) has only been made by separating some of the more striking dry types (D and parts of W on fig. 4). Much of the humid tropical burning depends on direct human intervention (Bartlett 1955, 1956; Batchelder 1967; Batchelder and Hirt 1966; Ramakrishnan this volume) and a refinement of groups and values should allow for this as well as for bioclimatic control, as by life zones.

Granting that both the estimates of areas covered and mean carbon burning per unit area require refinement, the products of these two variables can nevertheless be summed to estimate the potential annual global mean burning under recent ecosystem conditions (say 1925-1975 average?). My overall estimate is slightly less than $5 \times 10^{15} \text{ g C yr}^{-1}$ for global mean burning in table 3. This is a downward revision of my preliminary estimate, summing to $7(+4) \times 10^{15} \text{ g C yr}^{-1}$ (Baes and others 1976, Olson and others 1978). It seems more likely than not to be lowered further. The table focuses attention on the larger component numbers and subtotals which are likely to contribute most to any further revisions.

Among the Unesco formation groups I-V on table 3, ecosystem complexes dominated by closed forest (I), but including the appropriately interspersed types were estimated to contribute less carbon than open woodlands (II) and their closely associated tall scrub and savanna (1.27 vs. $1.71 \times 10^{15} \text{ g C yr}^{-1}$). Dwarf scrub (IV), including tundra, bogs, and heath, contribute much less than other scrub (III): 0.02 vs. 0.58 g C yr^{-1} , the latter mostly from shrub steppe and semidesert rather than extreme deserts (Humphrey 1958, 1963, 1974). Group V, dominated by crops and other herbaceous growth, with or without woody admixtures, may contribute as much as $1.4 \times 10^{15} \text{ g C yr}^{-1}$, roughly half in areas where farming or towns are very widespread (agro-urban).

To the right of these estimates and the corresponding mean flux per unit areas (both in parentheses on table 3) is a range of possibilities which is judged subjectively to span the true but unknown expected value for each regional ecosystem complex. A much wider span of regional values is given on the left of the ecosystem category mean per unit area. This span suggests the wide range of real variability, which has been discussed in many cases throughout earlier sections of this paper. Those ranges (see also legend of fig. 4) still are meant to apply to relatively large landscape blocks shown by map symbols (a big, but variable fraction of a degree of latitude and longitude). Variation for stands would be still wider: from near 0 to values somewhat higher than either of the upper ranges given on table 3.

SUMMARY AND CONCLUSIONS

The null hypothesis H_0 (table 1), that live and dead carbon accumulate during ecological succession to a steady state with little or no influence from fire, may apply in topographically protected areas of certain broadleaved forest and to some extreme conditions of high precipitation, low temperature, or consistently low precipitation or sparse cover, where amounts and continuity of available fuel or probabilities of ignition and fire spread are very low. The first alternative hypothesis H_1 is that carbon temporarily accumulates well above levels that can be sustained, but then tends to be reduced drastically in one or (commonly) two fires before long cycles of regrowth recur, as in many coniferous and mixed forest successions. Other conifer forests and many open woodlands, especially in monsoonal and Mediterranean-type climates, have evolved to favor and also to survive more frequent burning, which simply does not allow enough time for maximum regrowth of overstory and/or understory, under alternative hypothesis H_2 . Finally, alternative hypothesis H_3 covers extreme cases where very high fire frequency, with or without deterioration of the biological and nutritional potential for growth recovery, may keep phytomass and its residues relatively low almost indefinitely, as in many grasslands. Hence mean carbon loss rate from burning is lower despite high fire frequency. Possibilities that certain landscape units shift through several (sometimes all) of these regimes, and perhaps recycle more than once, have interesting implications for carbon and nutrient budgets, and for practical management of ecosystems.

As background for exploring those implications, differential equations describing these budgets are reviewed and then extended in terms of probabilities (table 2). These seem inherently more natural than deterministic models for chance events of burning and of some of the early- and late-season events of growth and translocation between fires under conditions of varying weather. A review of literature on ecosystem components and on several terms in the production side of the carbon budget leaves open issues about whether or not fire increases or diminishes the total carbon input rate significantly. With or without leaving a more or less open tree canopy overstory, burning generally favors herbaceous and shrubby life forms which are genetically programmed for short residence time of carbon and hence lower average and maximum carbon storage. Again decreasing the mean interval between fires offers more time for approaching a dynamic balance between the income and nonfire loss for nonwoody growth and, increasingly, for woody (or peaty) storage of carbon (fig. 1 and 2).

The trade-off between high burning frequency with low fuel available for burning vs. low frequency and high organic carbon accumulation is expressed quantitatively by the diagonal lines from upper left to lower right in each section of figure 3. SCOPE's fire studies need more cases where both variables were known, or even manipulated as in the experimental burns of grassy savanna in Kruger National Park (fig. 3b). I predict that tendencies for local variation to cluster around such lines would then become clearer than they are now.

The other diagonal contrast, from the high-burning lines on the upper right toward negligible burning in the lower left corner of each section of figure 3, guides our continuing search for better estimates of overall carbon flux of the biosphere. At least some of the savanna types (fig. 3B) have relatively greater areal extent than the Mediterranean scrub and associated woodlands, and may contribute $1.1 \times 10^{15} \text{ g yr}^{-1}$ of C, compared with $0.08 \times 10^{15} \text{ g C yr}^{-1}$. If similarly high release rates apply to other tropical drought-deciduous woodlands (foret claire) these might add another $0.4 \times 10^{15} \text{ g C yr}^{-1}$. Closed forests mostly burn less frequently (and have correspondingly higher inventory of live and dead fuels) but their large collective area may contribute almost $1.3 \times 10^{15} \text{ g yr}^{-1}$ of C.

There is a wide band of uncertainty around my interim estimates for these and all other parts of the global total. Adding all the low estimates and the high estimates, respectively, (i.e., assuming that errors did not compensate) gives a range of 3.2 to $6.8 \times 10^{15} \text{ g C yr}^{-1}$ (1 petagram, Pg, = $\times 10^9$ metric tons, or gigatons). These values are more likely than not to be skewed and perhaps biased high for various reasons. Hence, oxidation of nonfossil carbon is likely to be at least slightly or maybe considerably below the $5 \times 10^{15} \text{ g C yr}^{-1}$ released from the burning of fossil fuels in the mid-1970's. Whatever the true but unknown flux may be, closed forest, open woodlands, and closely associated savanna and scrub perhaps may contribute 60 percent of the total. It is still unclear how much of that oxidation is complete to CO_2 and how much remains, or is dispersed, as charcoal. Carbon monoxide is presumably a small fraction of the total C released.

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EFFECTS OF FIRE REGIMES ON BIOGEOCHEMICAL CYCLES

R. G. Woodmansee and L. S. Wallach

Associate Professor and Graduate Research Assistant
Department of Range Science
Colorado State University

ABSTRACT

The effects of fire on the biogeochemical cycles of ecosystems are considered: (1) the effects on the abiotic controlling factors (temperature, H-ion concentration, exchangeable bases, available water, and light); (2) the initial, or direct, effects; and (3) the postfire abiotic and biotic responses of ecosystems in general. The effects of fire on grasslands, deserts, forests, and tundras are compared throughout, and two emergent properties of the ecosystem are suggested.

KEYWORDS: biogeochemical cycles, conceptual models, ecosystems, fire, succession

INTRODUCTION

Fire can influence biogeochemical cycling in ecosystems in various ways, from stimulating growth and increasing nutritive value of forage in some grasslands to destroying not only vegetation but also entire soil-plant-animal-microorganism systems in some forested lands. The effects of fire on biogeochemical cycles are somewhat predictable, depending on the type and location of the ecosystem, the frequency and intensity of fire, and the frequency and intensity of meteorological events following fire.

Our objectives in this paper are to review key terrestrial ecosystem components and processes that may be affected by fire and to discuss important environmental factors that control the rates of processes. We will compare, in general, the effects of fire on various ecosystems and will propose some properties of ecosystems that may be unique to ecosystem-level biological organization.

GENERAL MODEL OF ECOSYSTEMS

Ecosystem response to fire is largely a function of both the responses of the individual organisms and abiotic controlling factors. The pathways of potential elemental transfer as a direct result of burning and the pathways that are highly susceptible

to postfire weather-related events are shown in figure 1. Vegetation greatly influences both fire intensity and postfire recovery; thus, an ecosystem's response to death of both roots and tops of vegetation will differ vastly from its response to death of tops only. Soil, physical, and chemical properties, presence or absence of litter, topography, and the stochastic nature of weather events also play important roles in determining the rates of nutrient transfers. Important pathways of elemental transfers in typical undisturbed ecosystems or systems that are successfully recovering from fire are shown in figure 2.

Not all the structural components represented in figures 1 and 2 contribute equally to all ecosystems, nor do processes within different ecosystems express equal rates of activity. Some of the processes shown in the figures rarely, if ever, occur in undisturbed ecosystems; but if the same systems are disturbed, normally dormant processes may be significantly activated. An example of such a process (series of processes) is nitrification. In some ecosystems nitrification or the potential for nitrification is well documented (Woodmansee in press), but in others the process is either nil or not important (Clark 1977, Woodmansee 1978, Gosz in press).

Our discussion is intended to be general and to represent transfers of many elements used by living organisms. However, most of our examples will relate to N because of its important growth-controlling role in most communities.

FIRE EFFECTS ON ABIOTIC CONTROLS IN ECOSYSTEMS

The effects of fire on abiotic factors controlling ecosystem functioning are critically important in subsequent ecosystem recovery. Many of these effects are discussed in detail elsewhere in this volume. We will briefly summarize those that seem especially important in explaining nutrient dynamics following fire.

Temperature

Two effects of fire on soil temperature must be considered: (1) the killing effect of heat during the fire and (2) the postfire effects of heat on physical and biological processes.

Though usually of short duration, high temperatures during fires significantly affect soil temperature and, consequently, the response of belowground organs and organisms. Heavy slash fires in coniferous forests are hottest, with recorded temperatures of about $1,000^{\circ}\text{C}$ just above the forest floor (Isaac and Hopkins 1937, Smith 1970); Isaac reported 320°C 1 inch below the surface. Stark (1977) categorized fire intensities for a Douglas-fir/larch community: Hot-burn temperatures are greater than 300°C at soil surface and all litter is consumed; medium-burn temperatures range from 180° to 300°C and half the litter is consumed; light-burn temperatures are less than 180°C and litter is only scorched. Fires in these categories generally kill plants and microorganisms. In contrast, Bentley and Fenner (1958) recorded temperatures of from 93° to 121°C at the soil surface of a grassland with light litter and of less than 93°C when heavy litter was present but unburned. In annual grassland, temperatures during fire ranged from 80° to 160°C at the soil surface and from 400° to 500°C a few inches above the surface (Williams personal communication). Average surface temperatures of chaparral/brushland fires are from 350° to 370°C (Bentley and Fenner 1958, DeBano and Conrad 1978).

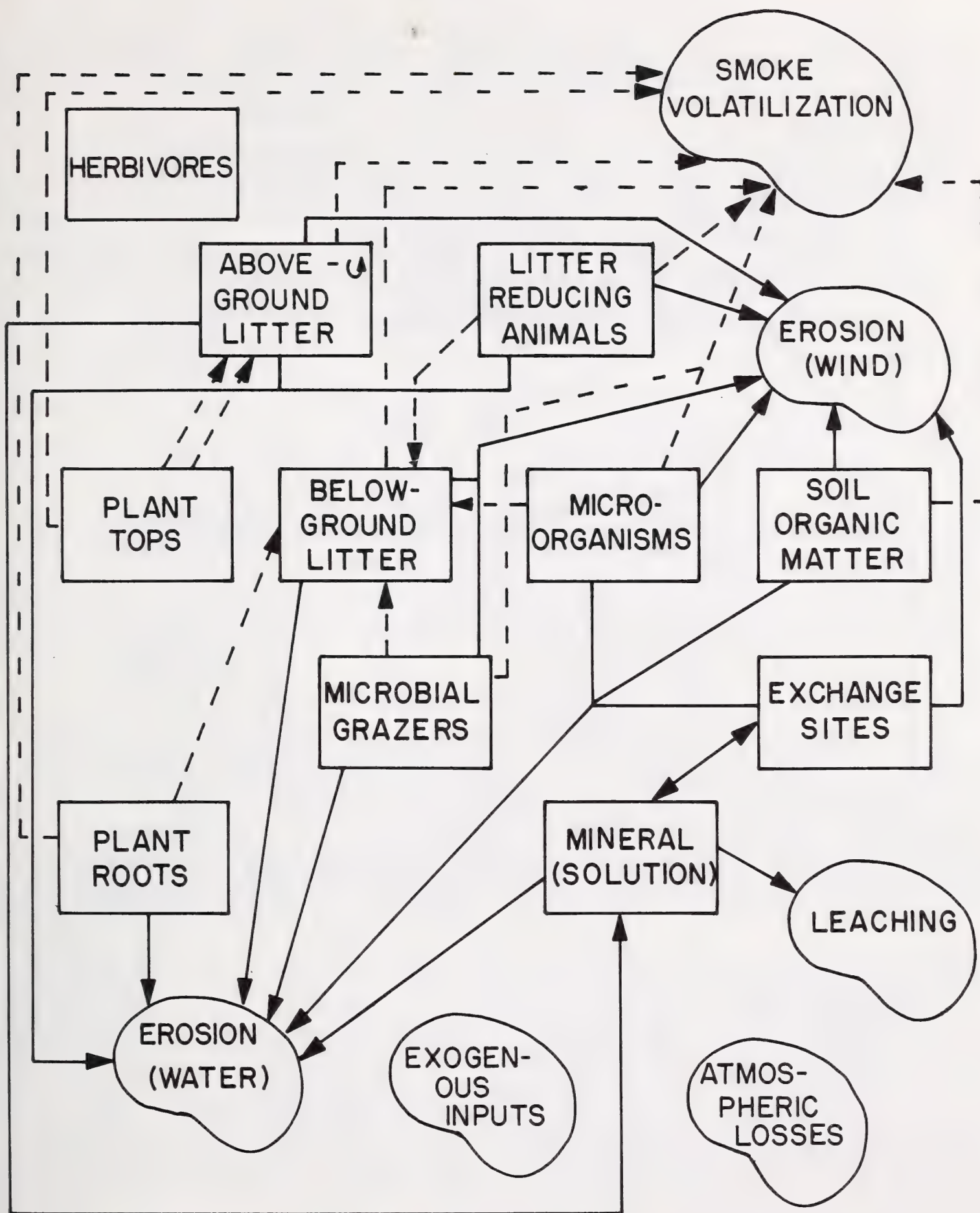


Figure 1.--Potential pathways of nitrogen transfers in an ecosystem affected by fire. Solid lines indicate the flows of elements that may occur following fire. Dotted lines indicate flows of elements that may occur as a direct result of burning.

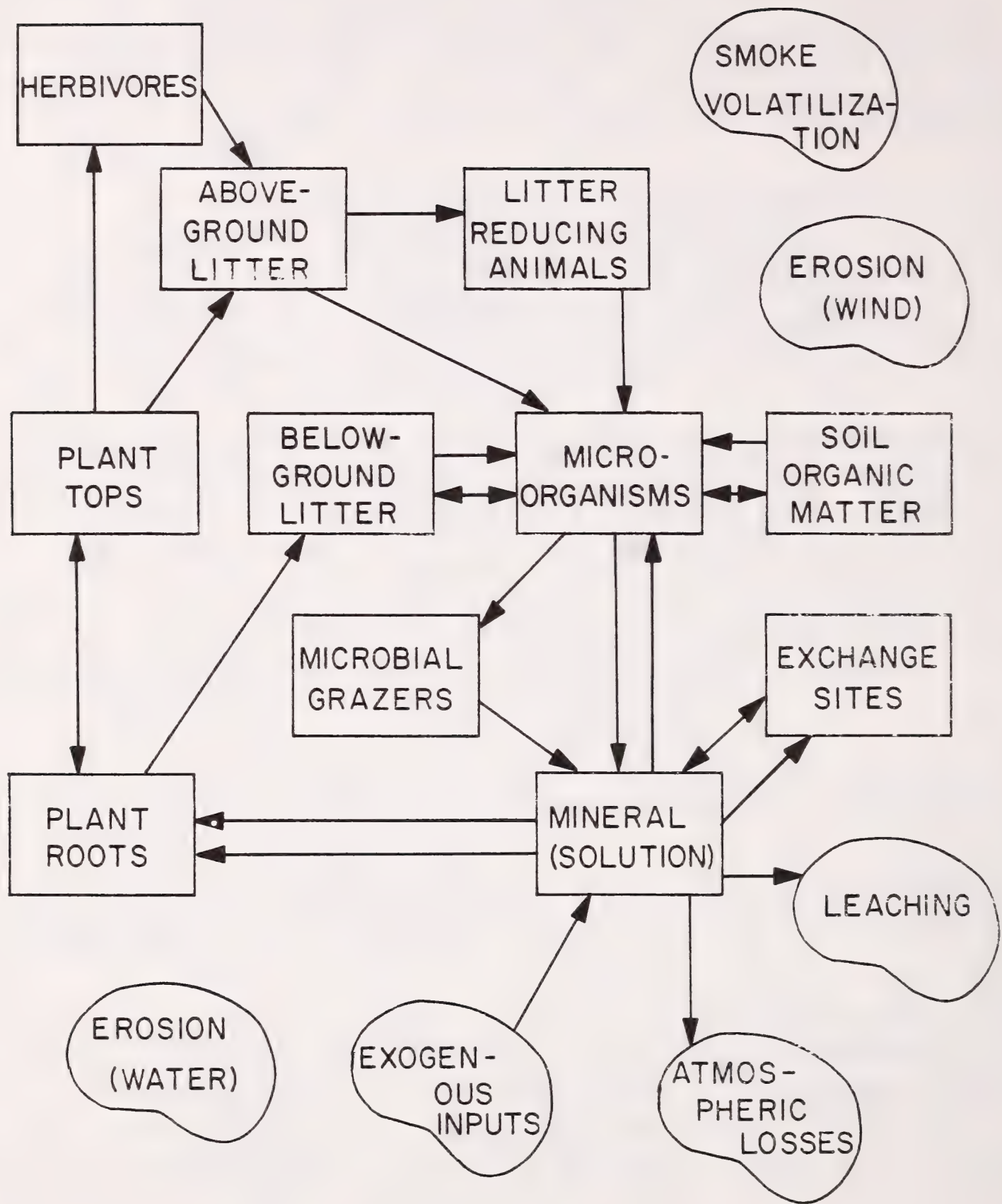


Figure 2.--Pathways of N movement in an undisturbed ecosystem.

Certainly, temperature alone is important, but the duration of high temperatures is also of concern. Of the ranges of temperatures cited, the lower values would be lethal only if sustained for several minutes or longer, while the higher values should kill most biota, even if maintained for short periods of time.

Fires can decrease cover, add charcoal to the surface, and darken the surface color. A decrease in cover exposes more soil to incident radiation and decreases surface insulation, while charcoal and a charred surface layer increase the absorptivity of the surface. These changes increase soil temperatures, which can influence biological activity. Postfire soil temperatures were 11°C higher at a depth of 5 cm in burned areas in the summertime in a Douglas-fir community (Neal and others 1965). For jack pine/black spruce communities, postfire temperatures averaged 6°C higher at a depth of 2.5 cm and 5°C higher at 7.5 cm (Scotter 1963). Postfire soil temperatures are consistently higher on burned than on unburned southwestern grasslands, 6° to 8°C higher at a depth of 2.5 cm (Daubenmire 1968). In a tobosa-grass (*Hilaria*) region, burned areas were 5°C warmer than controls at a depth of 7.5 cm (Sharrow and Wright 1977).

Postfire temperature changes in grasslands should be fairly short lived, whereas forested ecosystems take a long period of time to incorporate all the charcoal into the soil, to develop a ground cover of litter, and to establish prefire amounts of standing cover. During the recovery period soil temperatures may be significantly higher and, consequently, both biological and chemical processes may be more rapid than in unburned areas.

H-ion Concentration

Chemical analysis of postfire soil generally indicates that burning increases soil pH. Changes in soil pH can influence microbial activity (Alexander 1977) and are most evident in forested ecosystems, which tend to have more acidic soils (high H^{+} and Al^{+++} concentrations and low base saturation) and greater proportions of cations tied up in standing biomass than grasslands. Although changes in pH do occur in grasslands, they are not as significant as in forests, because the generally more alkaline soils of grasslands tend to buffer the effects of the changes.

The soil pH in a Douglas-fir community increased by 0.3 to 1.2 pH units following burning (Isaac and Hopkins 1937, Tarrant 1956, Neal and others 1965). The change in pH persisted for 1 year in the Neal and others (1965) study, whereas Tarrant (1956) found that after 1 year the pH had returned to near prefire levels. Wells (1971) reported that pH changed from 3.5 to 4.0 in the F and H horizons and from 4.2 to 4.6 in the top 5 cm of mineral soil after 20 years of burning on a very acid soil of a southern pine community. However, Christensen (1977) found no significant changes in pH in longleaf pine/wiregrass communities. In grasslands, pH changes of < 0.25 units are usually reported (Owensby and Wyrill 1973, Heyward 1936, W. A. Williams, pers. comm.), and DeBano and Conrad (1978) found no appreciable change in pH in a chaparral community.

Substantial shifts in pH can alter the activity of certain microorganisms (e.g., nitrifiers); change the rates of chemical reactions, making some elements more and others less available; and alter cation and anion exchange reactions. These pH changes may be short or long lived, depending on the leaching and surface erosion of the newly deposited bases. With high precipitation, pH changes tend to be short lived; but with low precipitation they should remain for a longer period of time.

Burning upsets the balance of exchangeable bases in the soil, generally greatly increasing their amounts on the surface immediately following a fire.

A threefold increase of Ca^{++} and a twofold increase of Mg^{++} (but no increase of K^+) in the humus layer of a coniferous forest was reported by Kozlowski and Ahlgren (1974). In the pine/wiregrass savanna, initial increases in extractable Ca^{++} , Mg^{++} , and K^+ were recorded following a fire, but prefire levels were evident 3 to 5 months later (Christensen 1977). Heyward (1936) reported twice as much "replaceable" Ca^{++} in the 0- to 7.5-cm layer of longleaf pine soil following fire. In another study in the longleaf region, all cations, but especially divalent Ca^{++} and Mg^{++} , were much more soluble as a result of burning (Lewis 1974). Similar results were reported for a ponderosa pine community (Fuller and others 1955), and Smith (1970) noted a 132 percent increase in soluble K^+ in the 0- to 2-cm soil layer in a jack pine community.

Greater amounts of exchangeable Mg^{++} , K^+ , and Ca^{++} were found in burned chaparral areas (DeBano and Conrad 1978), and Owensby and Wyrill (1973) concluded that winter burning resulted in the greatest increase in exchangeable bases in tallgrass prairie. In California annual grasslands, amounts of ash-derived exchangeable bases were small (W. A. Williams, personal communication).

Addition of exchangeable bases to soil surfaces not only increase concentrations of these nutrients but also, because of the higher concentrations, may increase the availability of some essential elements and raise pH, which in turn may stimulate some microbial (e.g., nitrification, N fixation) and plant activities.

Available Water

The higher temperatures can increase not only the rates of biological activities but also the rate of water evaporation. Soil moisture is directly reduced near the surface by evaporation during fire. By reducing the amount of organic matter in the surface layers of the soil, fire may also reduce the amount of water that can be held in these layers. Ash deposited at the surface and heat disruption of soil aggregates may also reduce the permeability of soils to water. Thus, by reducing cover, fire may increase runoff. Water that does not run off will percolate into the soil, where evaporation from the surface may increase. However, less water would be lost from the deeper soil layers because of decreased transpiration.

Heyward (1936) and Greene (1935), working independently, found no difference in water-holding capacity for a longleaf pine soil, but Greene found evidence that the burned area held more available water. Isaac and Hopkins (1937), studying fire in a Douglas-fir community, found that the available water was greatly reduced. Charcoal may slightly increase available water in sandy soil, has no effect in loam, and decreases available water in clay (Tyron 1948). Thus, charred humus may hold less water and may be less able to hinder evaporation than uncharred humus and, because burning increases temperatures, evaporation increases and available water decreases (Kozlowski and Ahlgren 1974).

Increased evaporation from the surface horizon reduces available water for microbial activity. Mineralization in the lower layers should be enhanced as a result of increased activity. Without transpiration, water may accumulate in the lower horizons, thereby increasing the probability of leaching ions from the profile.

Light

By reducing the amount of cover in forested areas, fire allows more light to reach the soil, which favors the regeneration of some species. Some grass and forb "sun-species" may flourish until shrubs and trees grow and suppress these shade-intolerant herbaceous species.

In an old spruce stand Kozlowski and Ahlgren (1974) found that grasses and herbs appeared first and spread rapidly following fire. Because of shading by trees, however, herbs began to decrease 6 years, and grasses 20 years, after burning, allowing shrubs (shade-tolerant species) to move in among the trees. Striffler and Mogren (1971) reported that 87 percent of species recorded in a postfire spruce/fir area were invading species, generally "sun-species" annuals.

Increased light at the soil surface may enhance activity of photosynthesizing and nitrogen-fixing microorganisms (Isichei and Sanford 1979, Jorgensen and Wells 1971).

GENERAL RESPONSES OF ECOSYSTEMS TO FIRE

We propose three general categories of ecosystem responses to fire: initial abiotic and biological, postfire abiotic, and postfire biological. Initial responses are the direct result of the effects of fire on ecosystem properties, postfire abiotic responses are the postfire effects of such events as runoff and wind erosion, and postfire biological responses are the effects largely mediated by biological processes.

Initial Abiotic and Biological Responses

The initial effects of fire on the biogeochemical cycles of ecosystems are: (1) the direct loss of elements to the atmosphere as volatilized compounds or as particulates carried away in smoke, (2) the release and transformation of ions and consequent deposition of ash elements on the surface, and (3) the response of individual organisms to the heat generated by the fire. The processes affected are shown in figure 1.

LOSSES TO THE ATMOSPHERE

During fire, considerable, but highly variable, amounts of ash elements and nitrogen are lost from ecosystems either in smoke or as volatilized gaseous compounds. Clearly, a fire that consumes all aboveground components of a typical grassland removes fewer elements than a fire that consumes a mature forest or shrubland (Rodin and Bazilevich 1967). However, the amounts of elements removed by a fire that consumes only the understory vegetation of a well-developed forest (e.g., a slash pine forest of the southeastern U.S. or an open ponderosa pine forest of the southwestern U.S.) and those removed by a fire on a typical grassland may be comparable. The chemical composition of the nutrients lost during fire has been described by Lloyd (1971), Lewis (1974), Grier (1975), and others, cited in Tiedemann (this volume).

The amounts of elements lost during a fire depend on many factors, including the biomass and elemental composition of aboveground vegetation and litter and the intensity and duration of the fire. Factors that influence fire intensity are described in section IV of this volume. Over long periods of time the frequency of fire also influences the amounts of elements lost. Therefore, frequent low-intensity fires may cause elemental loss that is comparable to infrequent high-intensity fires (Metz and others 1961, Foxx and Potter 1978).

ADDITION OF ASH TO ECOSYSTEM SURFACE

Ash elements derived from incinerated biomass are lost as particulates in smoke, are volatilized as gases, or fall to the surface as ashes. Elements in ashes are readily

available for uptake by plants or microorganisms but are also highly vulnerable to loss by water runoff or wind erosion (Tiedeman, this volume). Even though large amounts of elements are lost to the atmosphere as gases or in smoke, the elements that remain in ash, mostly oxides of metallic cations, are probably largely responsible for the often-reported luxuriant growth of vegetation shortly after a fire (Greene 1935, Daubenmire 1968, Owensby and Wyrill 1973, Sharrow and Wright 1977, Foxx and Potter 1978). Generally, much more than half of the ash elements, but less than half of the N, is returned to the soil surface from incinerated vegetation and litter.

RESPONSES OF INDIVIDUAL ORGANISMS TO FIRE

The importance of the relative resistances of vegetation to fire (Gill, this volume; Keeley, this volume) cannot be overemphasized when considering the response of biogeochemical capacity of an ecosystem to fire. When fire kills whole plants, destroying the metabolic capacity of both their aboveground and belowground portions, several important phenomena occur. As described, some elements in the aboveground portions are lost to the atmosphere and some are returned to the soil in ash. However, depending on the intensity of the fire, a sizable portion of biomass may be returned to the soil as uncombusted and freshly killed litter (Foxx and Potter 1978). Except for K, most elements in such litter are released only by microbial mineralization. Also, root systems of killed plants are large and important pools of elements, and some root fractions (e.g., unuberized roots, root hairs, mycorrhizae) are ready sources of easily mineralizable elements. Other, more resistant, root material is mineralized more slowly.

In contrast, when fire consumes only standing-dead vegetation and litter, the root systems remain viable and fully able to compete with microorganisms for nutrients released by the fire (Wright 1974).

Intermediate cases are those in which aerial portions of live plants are killed or injured but root systems survive to initiate subsequent resprouting of aerial organs.

Postfire Abiotic Responses

Abiotically controlled responses include loss of elements by wind and water erosion and leaching, release of elements from ash in solution, adsorption of ions onto exchange complexes, and volatilization of NH_3 from soils and litter (fig. 1).

WIND EROSION

Wind may remove nutrients in particulate debris, especially ash, from burned ecosystems. These losses could easily be large and significant if the amount of ash is large and the ground cover is sparse or nil. The hypothetical period of vulnerability of an ecosystem to wind erosion is shown in figure 3. We assume that ash is highly vulnerable to loss by wind immediately following fire. With time, plants resume growth, and wind erosion and loss of ash diminishes.

WATER EROSION

Losses of mineral forms of nutrients or relatively available nutrients (elements immobilized in organic matter) are controlled by many factors, some of which are discussed by Swanson (this volume), Grier (1975), Tiedemann (this volume), and Wright (this volume). Factors critically important in determining nutrient losses are the amount of ash deposited at the soil surface during fire; slope steepness; slope stability (which may be greatly influenced by the character of the residual root systems on the site); infiltration capacity of the soil; and, of course, the intensity, timing, duration, and form of precipitation following fire.

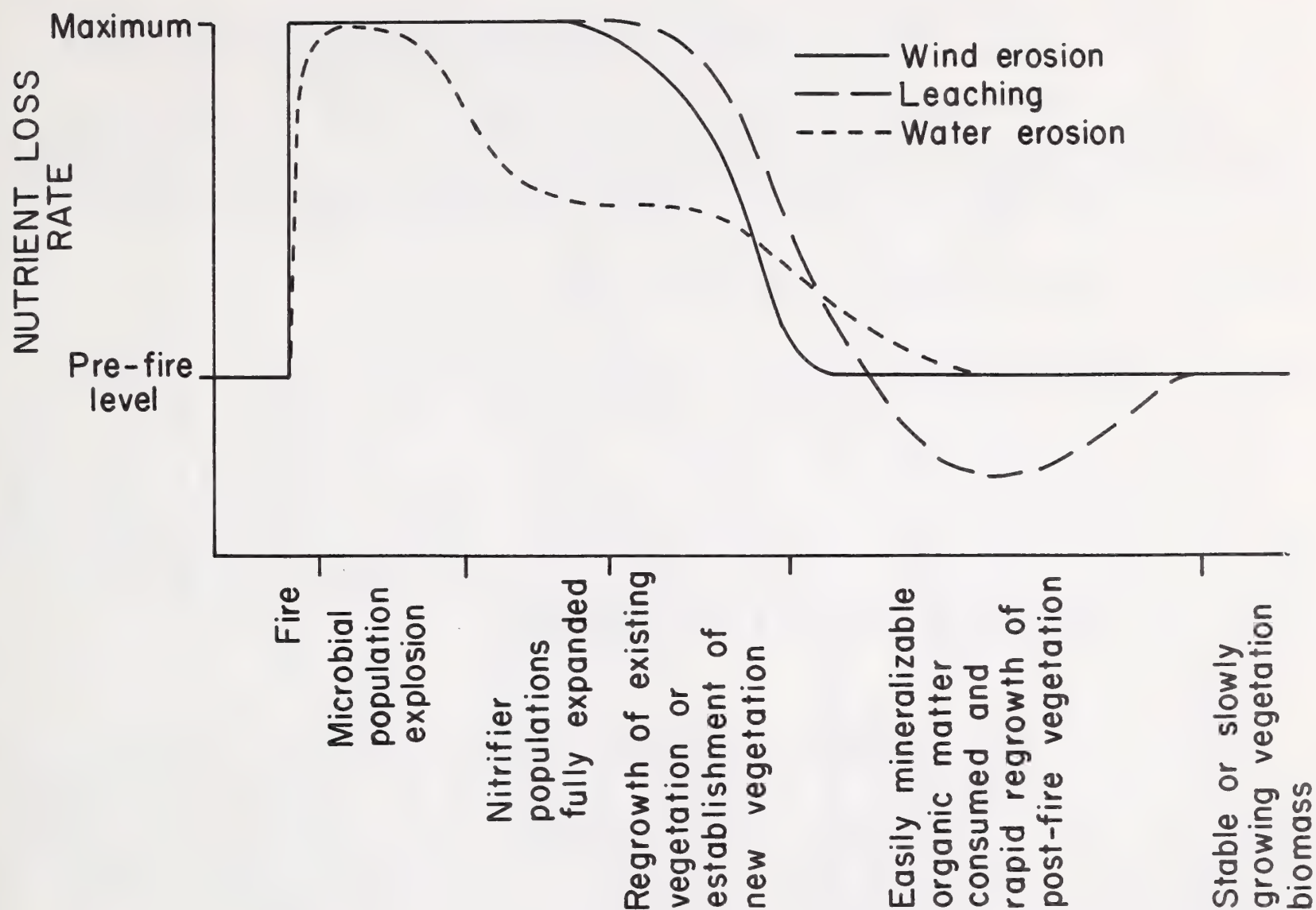


Figure 3.--Hypothetical potential for nutrient losses from an ecosystem following fire.

On steep slopes, ecosystems in which aboveground components and roots are killed and ashes are dispersed over the soil surface are highly vulnerable to large nutrient losses if precipitation is intense and runoff heavy. However, the same systems may lose few nutrients if precipitation is light and runoff small or nil. Ecosystems relatively undisturbed by fire (e.g., roots survive and some plant debris remains) certainly should lose fewer nutrients than those drastically disturbed (Gilmour and Cheney 1968, McColl and Grigal 1977). The period of principal vulnerability of water erosion is shown in figure 3. The second plateau corresponds to the period when root systems of former plants no longer maintain soil stability because of decomposition.

DISSOLUTION OF IONS

Nutrients in ash must be dissolved for uptake by roots or microorganisms (Tiedemann, this volume). In solution, ions not only are available for uptake but also are vulnerable to loss in surface runoff; may be leached into the soil profile (where they may be retained on exchange sites of soil colloids); may be leached completely through the soil profile and out of the root zone (especially if the roots have been killed); or, in the case of N, NH_4^+ may equilibrate with solution NH_3 and be ultimately lost to the atmosphere as gaseous NH_3 (Woodmansee and others 1979).

RETENTION ON SOIL COLLOIDS

Dissolved ions entering the soil profile may be retained by adsorption, depending on the cation exchange capacity, percent base saturation, and pH of the entire soil body. Deep soil, high in clay or colloidal organic matter but not saturated with Al^{+++} or Al hydroxides, probably retains most of the ions entering from the surface ash. Shallow soil, low in clay or organic matter content, retains few ions, with the excess being vulnerable to loss in runoff if sufficient water is present. Several studies illustrate the increase in base saturation of soil exchange sites following fire (Fuller and others 1955, Allen 1964, Lloyd 1971, Grier 1975).

LOSSES BY LEACHING OF IONS OUT OF THE ROOTING ZONE

Ions dissolved from ash can be lost to ground water if they occur in amounts in excess of exchange capacities of the soil (Wright, this volume). Numerous studies indicate that K^+ is the cation most vulnerable to loss by this pathway (Woodmansee and Innis 1973), followed by NH_4^+ , Mg^{++} , and Ca^{++} . We do not consider leaching of NO_3^- to be a secondary loss, because it is probably a product of biological activity subsequent to fire (Finn 1943, Stark 1977). The curve of leaching in figure 3 indicates a hypothetical pattern, in which ions added in ash and those released by mineralization are prone to pass through the soil system. The dip below prefire levels indicates the period of rapid plant development (Vitousek and Reiners 1975).

VOLATILIZATION OF NH_3

In some ecosystems, ash derived from fires contains some NH_4^+ ions in addition to relatively high concentrations of exchangeable bases (Neal and others 1965; Christensen 1973, 1977). If the concentration of NH_4^+ is relatively high at the soil surface and the surface pH is increased because of deposition of base-containing ash, NH_3 may be lost to the atmosphere as soils are wetted and dried (Woodmansee 1979).

Postfire Biological Responses

The biological responses to fire in various ecosystems are basically similar, the differences being the degree or rates of expression. The biological processes affected by fire are shown in figure 2, and the trends of various biological responses are shown in figures 4 and 5.

MINERALIZATION AND UPTAKE OF NUTRIENTS BY MICROORGANISMS

Following fire, microbial activity may be enhanced for various reasons, even though biomass near the soil surface is lost (fig. 4). In grasslands, dry tundras with little plant-residue accumulation, deserts, and forests where low-intensity surface fires occur, microbial activity may be only slightly enhanced and of short duration. Even though relatively small, increased rates of mineralization may be important in improving forage yield and protein content in vegetation of grazing lands (Owensby and Wyrill 1973).

Microbial dynamics and activity are profoundly changed in ecosystems drastically disturbed by fire (i.e., both aboveground and belowground parts killed). Under such conditions, processes such as N-fixation and nitrification may be considerably enhanced. Forests with high fuel loads are probably most likely to exhibit these changes.

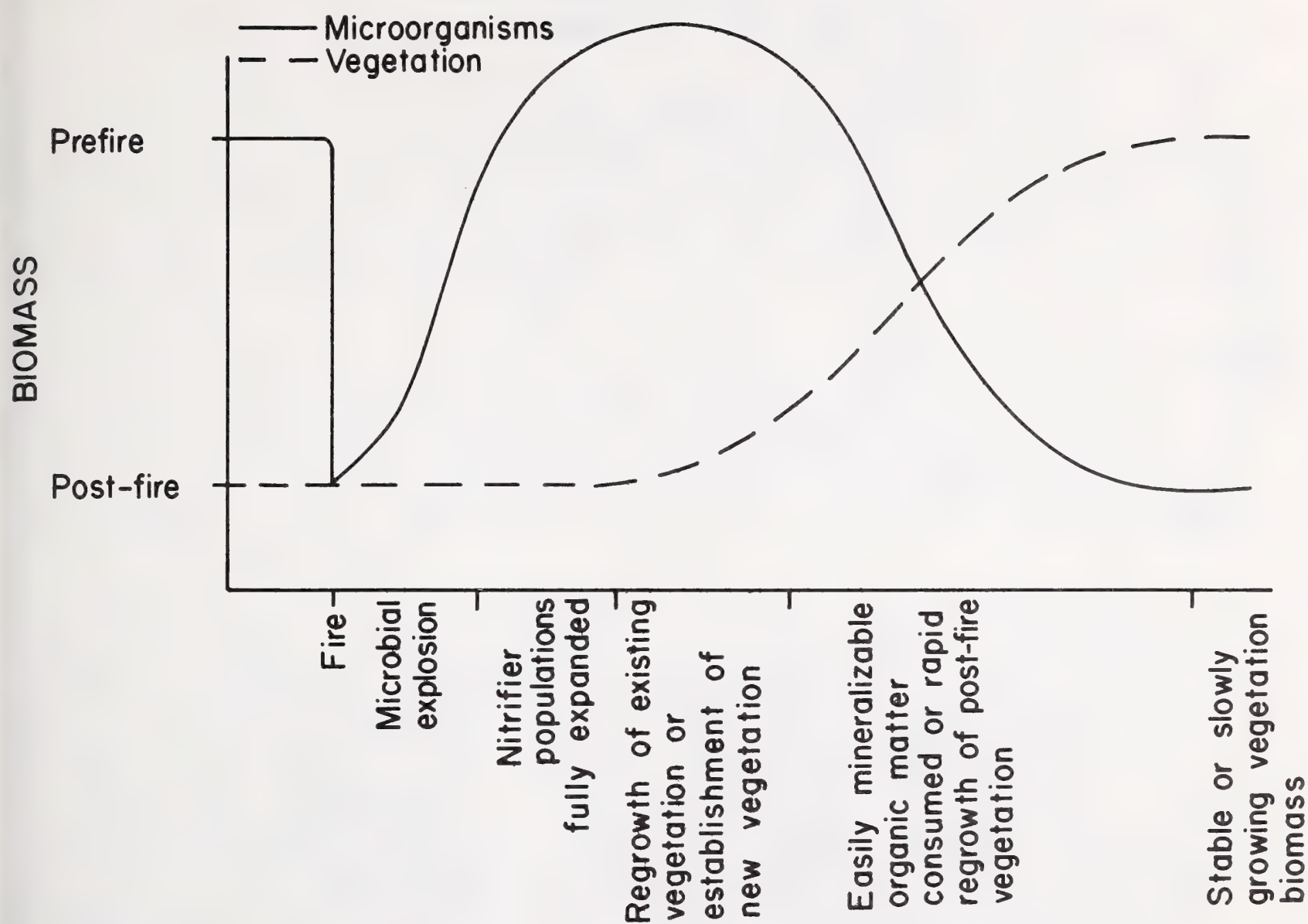


Figure 4.--Relative time course of nitrogen transformations in soils following fire.

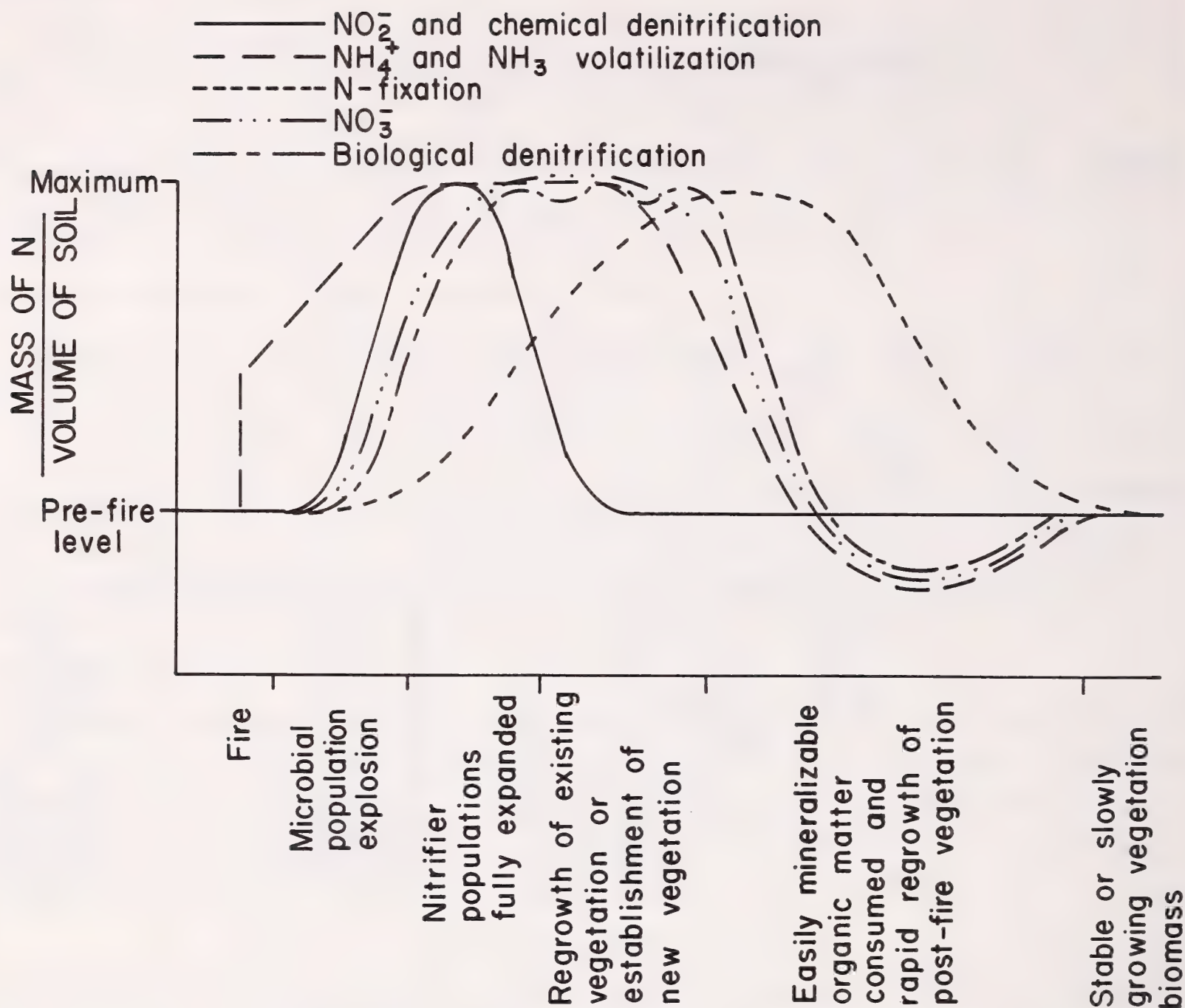


Figure 5.--Relative time course of hypothetical responses of organisms to fire.

UPTAKE OF NUTRIENTS BY PLANTS

Plant nutrient-uptake patterns following fire are discussed in detail by Chapin (this volume). Frequent and low-intensity burning in ecosystems whose vegetation is fire tolerant should not drastically alter uptake patterns. Rather, postfire response is an enhanced uptake of available forms of nutrients (especially N) mineralized by microorganisms or deposited at the soil surface in ash. However, non-fire-tolerant species may be destroyed and removed from the biogeochemical cycles.

Intense fires that kill large portions of whole plants or all vegetation drastically alter cycling patterns. Pioneer species (often annual or short-lived perennials) may become quickly established and immobilize large amounts of available nutrients, especially N. Benefits to the system are obvious. Nutrients are initially immobilized, then slowly released as more permanent vegetation becomes established and plant biomass becomes large enough to retain all available nutrients not retained by microorganisms. When vegetation is reestablished (fig. 4), leaching losses should be reduced to or below ambient levels (Vitousek and Reiners 1975).

NITROGEN TRANSFORMATIONS

Little nitrification and denitrification occurs in most ecosystems that contain viable root systems and living aerial portions of plants, mainly because of the rapid uptake of NH_4^+ by plants and microorganisms (Woodmansee 1978). However, with intense burning, excess NH_4^+ may be mineralized, followed by nitrification and denitrification (Fowells and Stephenson 1933; Tarrant 1956; Christensen 1973, 1977; Likens and others 1977). The sequence of these processes may be that indicated in figure 5. These conditions should be especially prevalent following tree-killing forest fires that do not consume N-containing organic residues.

Fixation of N_2 (fig. 5) into forms of N available for organisms is an important process in many drastically disturbed systems (Woodmansee and others 1979). In undisturbed native ecosystems the process may be unimportant. We assume that in some native, self-perpetuating ecosystems, fixation following low-intensity fires can contribute amounts of N of the same order of magnitude as deposition by wet or dry fall (Isichei and Sanford 1979), but such an estimate certainly has a wide range of variability.

Fixation of N_2 in drastically disturbed systems can be very large, greatly exceeding inputs from the atmosphere (Woodmansee and others 1979). In many innately productive (favorable soil water and temperature regimes) ecosystems, this pathway is critical to reconstruction of ecosystems. When this source of N is not present, centuries of atmospheric deposition might be required to replace N lost during or after fire. In highly productive forested regions of the country (e.g., Pacific Northwest, Southeast), N_2 fixation can be very large, leading to rapid reestablishment of vigorous, productive ecosystems. We postulate a strong relationship between climatic factors conducive to high productivity (such as high precipitation and warm temperatures) and the potential for rapid and significant development of N-fixing organisms. After a severe fire in the Pacific Northwest, for example, Ceanothus spp. or Alnus spp. may invade a site and fix copious amounts of N. In regions with much lower productivity (for example, the central Rocky Mountains), the amount of N fixed is undoubtedly much lower, even though N-fixing organisms characteristically invade drastically disturbed areas (Woodmansee and others 1979).

COMPARATIVE ANALYSIS OF ECOSYSTEM RESPONSES TO FIRE

Initial Abiotic and Biological Responses

Ecosystems having a preponderance of biomass and nutrients in belowground organs or debris (grasslands, tundra, deserts) are generally less severely disturbed by fire than those having a large proportion of nutrients tied up in aerial biomass, if that aboveground portion is consumed by fire. This generalization is especially true for N because it can be transformed to gas and lost from the system (fig. 1). For example, typical amounts of N contained in aboveground portions of grasslands may range from < 10 to 30 kg ha^{-1} , depending on available fuel and fire intensity. Consequently, losses of N by fire are relatively small in grasslands and can be expected to be replaced by atmospheric deposition or low-level N_2 fixation within 1 to 6 years (Isichei and Sanford 1979, Risser and others in press, Woodmansee and others 1979). Likewise, fire in either tundra with mineral soils or arid-zone ecosystems with low productivity would be expected to lose only small quantities of N or other nutrients from burned aerial parts or litter. Recovery of N losses may take longer, however, because tundra and arid zones receive smaller amounts of nutrients from the atmosphere than many grasslands (Junge 1958; Woodmansee 1978, 1979).

When low-intensity fires consume only ground vegetation and small amounts of litter, forests probably recover lost nutrients from the atmosphere or by ambient N_2 fixation within a few to several years. For example, Gosz (in press) estimated that 5 to 10 kg ha⁻¹ yr⁻¹ mineral-N may be added from the atmosphere alone by wet and dry deposition. In the same region, Foxx and Potter (1978) estimated a fire frequency of about 17 years in southwestern semiarid forests, before man began suppressing fires. Thus, in 17 years, 85 to 170 kg N ha⁻¹ would be added to such ecosystems, probably more N than is consumed by a low-intensity fire.

Low-intensity surface fires are a management tool in forests in the southeastern United States (Metz and others 1961, Moehring and others 1967), where N lost by fire (fig. 1) may be replaced rapidly by N_2 fixation (fig. 2) by legumes and nonsymbiotic organisms (Jorgensen and Wells 1971).²

We assume that in low-intensity fires nutrients other than N are mostly returned in ash to the soil surface, where they are quickly leached into the soil and utilized by organisms or adsorbed onto soil colloids until taken up by organisms. We also assume that during low-intensity fires in ecosystems few if any plants are killed. Thus, nutrient uptake by vegetation is not significantly impaired.

Ecosystems having large amounts of nutrients in aboveground aerial portions of plants or in rich organic layers are quite vulnerable to catastrophic losses of nutrients. Not only are nutrients more exposed to combustion but also, because of the large amounts of organic matter aboveground, the probability of high-intensity, totally consuming fires is much greater. Large amounts (up to 80 percent) of gaseous N and other elements may be lost in smoke from such high-intensity fires (Isaac and Hopkins 1937, Fuller and others 1955, Moore 1960, DeBell and Ralston 1970). Replacement of nutrients lost during combustion may take decades by atmospheric deposition alone. This type of catastrophic loss is aggravated by man's attempts to control fire, which allow debris to accumulate in many forests (Wright and Heinzelman 1973).

Postfire Abiotic Responses

Ecosystems having a small proportion of their biomass aboveground or those in which only the understory vegetation is consumed by fire suffer relatively little disruption of abiotically controlled portions of biogeochemical cycles. In these systems some increase in wind and water erosion might be expected for a brief period following fire but should be short lived. Thus, erosion would not be expected to deplete large amounts of nutrients. Leaching losses remain low because plants are generally not killed and the integrity of the soil is maintained by large concentrations of roots. Only relatively small quantities of nutrients are involved in combustion; therefore, those returned in ash and solubilized may be rapidly and completely utilized by organisms (if the amounts deposited do not exceed the uptake capacity of the organisms).

In systems where high-intensity fires occur, especially if root systems are killed, postfire losses of nutrients may be large if precipitation is heavy or wind is strong. Such losses are highly probable in forests whose trees are killed, especially on steep slope and in areas exposed to wind. The importance of the stochastic nature of weather events cannot be overstated. High-intensity or long-duration rainstorms or rapid snowmelt on a severely burned ecosystem can greatly disrupt the soil, with catastrophic effects. We emphasize the point that fire in ecosystems infrequently burned and with accumulated biomass can be catastrophic, greatly altering the patterns of biogeochemical cycling. This is especially true if the integrity of the soil-microorganism-animal-plant root system is disrupted. If precipitation is not heavy, disruption should be slight and nutrient losses small.

Fire can profoundly alter the patterns and amounts of nutrient uptake by microorganisms and plants; the rates of decomposition, mineralization, nitrification (and possible leaching of NO_3^-); the occurrence of denitrification; the potential losses of gaseous NH_3 from mineralized organic matter; and N-fixation rates. As discussed, the key controlling factors of these processes are temperature, pH, nutrients (such as exchangeable bases) added in ash, available water, and light. Fire tolerance of individual organisms and the dynamics of populations or organisms also affect ecosystem response to fire.

MINERALIZATION AND UPTAKE OF NUTRIENTS BY MICROORGANISMS

Typically, fire stimulates the activity of soil microorganisms (Ahlgren and Ahlgren 1965, Jorgensen and Hodges 1970, Risser and others in press). Following high-intensity fires where both above- and belowground vegetation are killed, microorganisms have a new and large source of carbon from deep root systems and residual aboveground litter; often more favorable growing conditions, because of the higher soil temperatures resulting from increased incident radiation (Greene 1935, Lloyd 1971); often more favorable pH (Fowells and Stephenson 1933, Neal and others 1965); greater amounts of available nutrients in ionic form, from ash (Ahlgren and Ahlgren 1965, Gilmour and Cheney 1968); and more available soil water (Jorgensen and Wells 1971), in the absence of transpiring plants. Combined, these factors enhance uptake of nutrients by microbial populations. Dramatic examples of this phenomenon have been found in forests of the Pacific Northwest, where the nutrient content in charcoal and boles in fallen trees increased, presumably because of the ingrowth of fungal mycelia from underlying soils (Kermit Cromack, personal communication).

Agronomists call this uptake process immobilization, usually implying its undesirability. Ecologists, however, should view immobilization as the "salvation" of nutrient pools in drastically disturbed ecosystems. For, while microorganisms may be decreasing nutrient flow to developing or regenerating vegetation, they are also retarding nutrient losses from the ecosystem. Eventually, as root-carbon sources are depleted by microorganisms, net mineralization will commence, to the benefit of recovering vegetation. However, even before carbon sources are reduced to net mineralization levels, significant amounts of nutrients (e.g., N and P) may be released into solution as waste products of microbial grazers (Coleman and others 1978). Microorganisms and developing plants will compete for those ions. Thus, microorganisms may not immobilize all nutrients; some may be available for uptake by plants, and some may be lost by leaching. In many cases, redeveloping vegetation may be quite efficient in taking up ions and will produce luxurious and protein-rich growth (Fowells and Stephenson 1933, Ahlgren and Ahlgren 1960, Christensen 1977).

Risser and others (in press) suggested that microbial activity is enhanced if low-intensity fires do not kill substantial amounts of vegetation. The simplest explanations for this enhancement are that removal of shading by standing-dead plant material or litter increases soil temperature and, possibly, that reduced interception by plant debris slightly increases soil water. Under these conditions, mineralization rates increase (Neal and others 1965, Christensen 1973), increasing amounts of available nutrients and, consequently, plant productivity or nutrient content (Owensby and Wyrill 1973, Christensen 1977, Risser and others in press).

Nutrient availability may be enhanced in spite of the net loss of nutrients from the community caused by initial or subsequent effects of fire. This is especially apparent for N. Large amounts of N may be lost by combustion, yet subsequent vegetation response may be very favorable, showing increased aboveground production and forage quality (Vlams and others 1955, Knight 1966, Grier 1975, Sharrow and Wright 1977).

If sufficiently high concentrations of NH_4^+ are produced by mineralization or microbial grazing near the surface of the soil, NH_3 may be lost in significant amounts (Woodmansee 1979).

UPTAKE OF NUTRIENTS BY PLANTS

When fire kills all vegetation in an ecosystem, uptake of nutrients by plants will not occur until vegetation is reestablished. Revegetation as a process is dealt with elsewhere in this volume. However, the rate of revegetation is critical in determining the nutrient-retention characteristics of the ecosystem.

If revegetation is rapid, the potential for postfire loss of the nutrients will be reduced and the loss-retarding mechanism of microbial uptake will remain effective (fig. 4 and 5). However, if revegetation is retarded, catastrophic amounts of nutrients may be lost because of the increased probability of severe erosion. Furthermore, with slow vegetation recovery, microorganisms may eventually deplete their carbon sources, net mineralization will occur, exchange sites may become saturated, and leaching losses may ensue (given sufficient precipitation).

When fire does not kill all the roots, ecosystems may retain sufficient capacity to take up all or large portions of available nutrients released by dissolution of ash elements or by mineralization. We postulate that many plants may respond to "wounding" by fire with increased rates of nutrient uptake. Such wound responses may be similar to enhanced growth responses to grazing or clipping of vegetation (M. I. Dyer and others, unpubl. data).

Some species of plants in burned communities are favored by increased water and light availability resulting from fire. Such species compete for, and successfully capture, many nutrients from the soil solution and show increased vigor compared with previously or potentially dominant plants (e.g., the tallgrass prairie--eastern deciduous forest tension zone). In the absence of fire many such species may be suppressed or eliminated by fire-tolerant species.

NITROGEN TRANSFORMATIONS

Nitrogen is an interesting element in ecosystems, not only because it is a major constituent of biomass, but also because it has an open cycle and is therefore very dynamic (Woodmansee 1978). It is the principal limiting element in most native terrestrial ecosystems. Its dynamic nature is attributable largely to potential, though ephemeral, biological transformations associated with its transfer through ecosystems. We have discussed nitrogen in general terms along with other elements because in its cationic form, NH_4^+ , its behavior is similar to that of other cations. Following severe disturbances like fire, however, several N processes may be altered, possibly resulting in biologically mediated losses (such as leaching of NO_3^- or denitrification) or additions (such as N-fixation).

Nitrification, Denitrification, and Leaching

Some native ecosystems nitrify NH_4^+ and some do not. In most undisturbed native systems (except urine patches), NO_3^- occurs in only very low concentrations (Clark 1977, Woodmansee 1978, Woodmansee and others 1978, Gosz in press, Vitousek and others 1979). Deserts and some deciduous forest ecosystems (e.g., aspen stands) also may be exceptions to this rule (Gosz in press). Causes for the different potentials for nitrification in undisturbed systems are discussed by Vitousek and others (1979).

Burning can enhance nitrification, probably because it creates favorable environments (e.g., more favorable temperatures and soil water, possibly higher pH values, and excess NH_4^+) for nitrifying organisms (Fowells and Stephenson 1933; Neal and others 1965; Christensen 1973, 1977). During nitrification, NO_2^- may be transformed (fig. 5) to NO_2 or NO and possibly on to N_2O and N_2 by chemical denitrification (Clark 1962, Focht and Verstraete 1977). The importance of this process as a result of burning is unknown.

Once formed, the NO_3^- is available for uptake by organisms. If not taken up and utilized for biomass production, it may be lost from the system in percolating water; or, if water is insufficient to carry the NO_3^- ions out of the rooting zone, it may simply remain in solution (Finn 1943, Tiedemann and Helvey 1973, Stark 1977). If NO_3^- remains in solution and soil conditions become favorable for biological denitrification (e.g., those mentioned for nitrification, available organic substrate, and low O_2 potentials), N may be lost as N_2O or N_2 (Focht and Verstraete 1977).

Fixation of N_2

Most native ecosystems appear to contain, or have the potential for producing, organisms capable of converting atmospheric N_2 to biologically bonded N in biomass. The literature on this subject is extensive.

We postulate that ecosystems tending to be N limited (e.g., N limits production of biomass) have a strong potential for developing organisms capable of fixing N_2 . For example, according to Dodd and Lauenroth (1979), native and introduced legume populations greatly increased in shortgrass prairie where irrigation supplied the principal limiting factor, water. These authors postulated that available N supplies were greatly diluted by a large increase in total biomass, causing N limitations to be expressed. Annual grasslands appear to be periodically depleted of available N, probably as a result of NH_3 losses (Woodmansee and Duncan, in press; Jones and Woodmansee 1979). When N depletion is expressed, herbage production (principally grasses) decreases, and legumes, which can then compete for incident radiation, accelerate growth and fix relatively large amounts of N_2 . Lands drastically disturbed by such disruptions as surface mining are frequently colonized by N-fixing organisms (Woodmansee and others 1979), and ecosystems severely depleted of N by fire often are revegetated by N-fixing organisms (Youngberg and Wollum 1970, Grier 1975, Foxx and Potter 1978).

We do not want to imply that fixation occurs only in ecosystems severely limited by N. All terrestrial biomes include ecosystems that contain either symbiotic or nonsymbiotic N_2 fixers that can supply significant amounts of biologically available N under favorable conditions.

We do imply, however, that in ecosystems depleted of N by fire, N_2 fixation can be a very important N-replenishing mechanism without which ecosystem recovery would take decades or centuries (Woodmansee and others 1979).

EMERGENT PROPERTIES OF COMMUNITIES

Ecosystems universally seem to exhibit properties unique to that level of biological organization. We will briefly discuss two of those properties in summarizing our discussion: the propensity to retain nutrients following fire and the propensity to quickly replace N if large amounts are lost as a result of fire.

Several mechanisms are involved in nutrient retention in ecosystems following fire. Some vegetation may tend to retain nutrients even before fire (e.g., translocation of nutrients from aboveground to belowground parts at senescence, especially in grasslands). Following fire, ash deposited at the soil surface contains cations and anions that can be readily lost in solution from an ecosystem (fig. 3). However, as those ions leach into the soil layers, they tend to be adsorbed on ion exchange complexes associated with organic matter and clay colloids, which delays their movement out of the zone of biological activity. Shortly after favorable soil-water conditions are established, microbial activity and any remaining live-root activity tends to immobilize nutrients from solution for biomass production (fig. 4). If the vegetation cover is substantially destroyed by fire, "pioneer" species of plants may germinate, grow rapidly, and take up large quantities of nutrients. Following these events, more permanent vegetation-microorganism-animal systems develop that can efficiently utilize the nutrients mineralized from the large populations of microorganisms and pioneer plants.

This sequence of events (both biotic and abiotic) following fire is consistent with hypotheses of nutrient retention by ecosystems presented by Vitousek and Reiners (1975) and Woodmansee (1978), who suggest that nutrient retention by early seral communities may be very efficient (fig. 3 and 5).

Nitrogen recovery and mobilization may also be properties unique to the ecosystem level of organization. Microorganism populations responsible for mineralizing N (and other nutrients) are frequently stimulated by environmental conditions that follow fire (fig. 4). Organisms thus stimulated may mineralize N in resistant soil organic matter (Clark 1977, Woodmansee and others 1978) faster than before fire.

Nitrogen-fixing microorganisms often seem to be stimulated by fire (Jorgensen and Wells 1971, Moore 1960, Isichei and Sanford 1979). In many systems they contribute enough available N to rapidly replace lost N and, in some cases, to increase soil N. Often the so-called pioneer species mentioned are N-fixers. In ecosystems with high productivity potential, amounts of N thus fixed can be large.

The two emergent properties proposed may belong to a much larger set of responses of entire ecosystems to fire or other drastic disturbance. Both properties are combinations of abiotic and biotic components and processes that occur in both time and space. Consequently, even though a given component or process may seem to be quite unrelated to some other in either time or space, combined they may produce properties unique to ecosystems and ecosystem development.

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FIRE AND GEOMORPHIC PROCESSES

Frederick J. Swanson

Research Geologist

U.S. Department of Agriculture, Forest Service
Pacific Northwest Forest and Range Experiment Station

ABSTRACT

Fire, geomorphic processes, and landforms interact to determine natural patterns of ecosystems over landscapes. Fire alters vegetation and soil properties which change soil and sediment movement through watersheds. Landforms affect fire behavior and form firebreaks which determine burn boundaries. Geomorphic consequences of fire in a landscape-ecosystem type are determined by (a) characteristics of the fire regime, mainly frequency and intensity; and (b) geomorphic sensitivity or erodibility of the landscape.

KEYWORDS: fire, erosion, watershed management, sedimentation

INTRODUCTION

Fire, geomorphic processes, and landforms interact in a variety of ways that are important determinants of patterns of natural ecosystems over landscapes. Many relationships between fire and geomorphic factors are mediated by vegetation, soil properties, and hydrology. Fire alters vegetation and soil properties; these changes alter the hydrologic regime of a site with the collective effect of changing the movement of soil and sediment through watersheds. Landforms and the long-term operation of processes that shape them influence soil distribution, microclimate, and other factors that control distribution of plant communities on a landscape. By their temporal and spatial patterns of fuel loading, plant communities influence the fire regime of a site.

Types and intensities of these fire-geomorphic factor interactions vary with the time scale at which a landscape-ecosystem unit is viewed. On the short-term scale of landscape-ecosystem response to a single fire, fire affects geomorphic processes through alteration of vegetation, soil, and hydrology. These interactions are most important in fire-prone ecosystems in steep terrain where vegetation regulates physical processes. In the much longer time frame of landscape development the sense of this relationship is reversed. Landforms, especially in areas of high relief, may strongly influence fire behavior and pattern by effects of topography and fire breaks. Vegetation-landscape patterns viewed at any point in time reflect both short- and long-term relations among fire, vegetation, soil, hydrology, and geomorphic factors.

The type of broad perspective studies necessary to evaluate interactions between fire and geomorphic factors in an ecosystem context are rare. The few studies of erosional consequences of fire have been narrow in scope, lacking ecosystem perspective and failing to examine long-term implications of short-term observations. In an effort to expand on these narrow views, Wright (1974) examined geomorphic systems and ecosystems over the time scales of landscape development and plant community change by succession and migration. Reviewing examples from the Appalachian Mountains (Goodlett 1954, Hack and Goodlett 1960) and the Boundary Waters Canoe Area, northern Minnesota (Ohmann and Ream 1971, Heinselman 1973), Wright (1974) saw weak interaction between fire and geomorphic factors. Forests in the steep Appalachian Mountain site experience very infrequent fires but are sensitive to disturbance by erosion and windthrow events. Fire is a controlling factor in vegetation patterning in the northern Minnesota example, but low relief and resistant bedrock result in low erosion potential even after fire.

These two areas do not dramatically express interactions between fire and geomorphic factors, but they do highlight the variables that control these interactions: fire regime, geomorphic sensitivity to vegetation disturbance, and topography. Youthful landscapes with steeper terrain and greater relief have greater sensitivity to fire disturbance. They exhibit more vegetation zonation in response to topography, more active contemporary geomorphic processes that may be subject to vegetation control and acceleration by fire, and greater effect of topography on fire behavior. In these landscapes we can identify such relationships; perhaps when they are better understood we can observe these relationships where they are more subtle.

This paper reviews research on effects of fire on geomorphic processes and sediment yield from watersheds and effects of landforms on fire behavior and pattern. Conceptual approaches with limited examples are presented for analyzing effects of fire on sediment yield over several fire rotations and for contrasting the geomorphic significance of fire in diverse landscape-ecosystem types. However, we begin with a general discussion of soil and sediment routing through watersheds to set a basis for evaluating fire effects on geomorphic systems.

SOIL-SEDIMENT ROUTING

In order to evaluate fire effects on geomorphic processes in an ecosystem, it is necessary to understand the roles of vegetation in regulating soil-sediment routing through watersheds (Dietrich and Dunne 1978, Swanson and others in press). Soil is moved down hillslopes by a variety of mass movement and surface erosion processes. Once in the channel, this material, now termed sediment, is moved downstream by another set of transfer processes. A given particle of material moves through a watershed in a series of steps by different processes, and it may be moved by several processes simultaneously.

During its transit through a watershed, material is temporarily stored in various types of storage sites (Dietrich and Dunne 1978). Down logs in forest ecosystems, for example, trap material moved downslope by surface erosion processes and downstream by channel processes of particulate matter transfer. Sediment is also stored in alluvial fans, flood plains, and in-channel sediment deposits. Residence time of material in storage sites ranges from days to thousands of years (Dietrich and Dunne 1978).

Vegetation affects the rate of each transfer process and the capacity and turnover time of storage sites. Root networks bind soil, thereby reducing mass movement potential from slopes and stabilizing flood-plain deposits; organic litter protects soil from surface erosion; blowdown of trees causes soil movement, but the down logs form storage sites. These and other factors result in complex response of soil-sediment routing systems to ecosystem disturbance. Since each geomorphic process is regulated by a different set of vegetation factors, each process will recover to predisturbance rates over different time periods, determined in part by the pace of vegetation recovery.

As a result of these vegetation-geomorphic process interactions, destruction of living and dead fuels by fire may alter all components of the soil-sediment routing system of a watershed. On the other hand, just as fire can selectively affect species or vegetation strata, it can also selectively alter components of the soil-sediment routing system. Low-intensity fire, for example, may reduce ground cover, and cause accelerated surface erosion while having no effect on rooting strength and mass movement potential. Although most fire effects research has concentrated on acceleration of individual transfer processes and total sediment yield from drainage basins, fire-induced sediment yield reflects changes in both transfer processes and storage.

SHORT-TERM FIRE EFFECTS

On the time scale of watershed ecosystem response to a single fire, fire works through alteration of vegetation, soil properties, and hydrology to trigger immediate and delayed changes in geomorphic processes on hillslopes and in channels. Many of the complex interactions among fire, vegetation, soil, hydrology, and geomorphic processes are summarized in figure 1. Although this summarization leaves out many details, generalizes where some important exceptions may arise, and covers a broad range of processes that do not all operate in any single environment, it is used as the basis for the following discussion. This discussion concerns mainly wildfire effects on natural vegetation. Effects of slash and prescribed burning are compounded and obscured by impacts of other management activities.

Fire Effects During Burning

Records of geomorphic processes immediately during fire are based almost entirely on personal communications and popular accounts of major fires. Intense drying of soil, combustion of organic matter that binds soil aggregates, loss of litter cover, and strong convective winds produced by the fire's heat all contribute to debris movement down steep slopes during hot fires. In steep terrain, rolling rocks and logs released by burning of roots and other supportive organic matter endanger firefighters and trigger downslope movement of other material. Strong winds in very intense fires have caused extensive blowdown (Holbrook 1943, Cohen and Miller 1978, Felt 1978), leading to formation of large areas of pit and mound microtopography. This phenomenon also greatly increases concentration of large woody debris on slopes and in stream channels which affect movement of soil and sediment.

Rock materials exposed at the ground surface as outcrops or cobbles and boulders may shatter and spall in response to direct differential thermal effects and vaporization of interstitial water. These processes of rock degradation reduce the particle size and persistence of boulder fields and accelerate soil forming processes (Blackwelder 1927, Birkeland 1974).

Recent research on fire alteration of soil properties focuses on formation of hydrophobic soil properties, especially in chaparral vegetation (DeBano and others 1977). This work involves monitoring the thermal regime of the upper portion of the soil profile during burning. Steep thermal gradients occur in the upper few centimeters to decimeters of soil beneath fire. Vaporization and transfer of water across the gradient are instrumental in movement of other compounds. Under these conditions an efficient distillation process leads to coating of soil particles below the surface with nonwetable organic compounds.

Delayed Fire Effects

In contrast to the poor documentation and quantification of immediate fire effects on geomorphic processes, effects of fire on hydrology and geomorphology following burning have been studied in some detail. Most fire-initiated changes in hydrology and geomorphic processes take place over periods of up to decades following

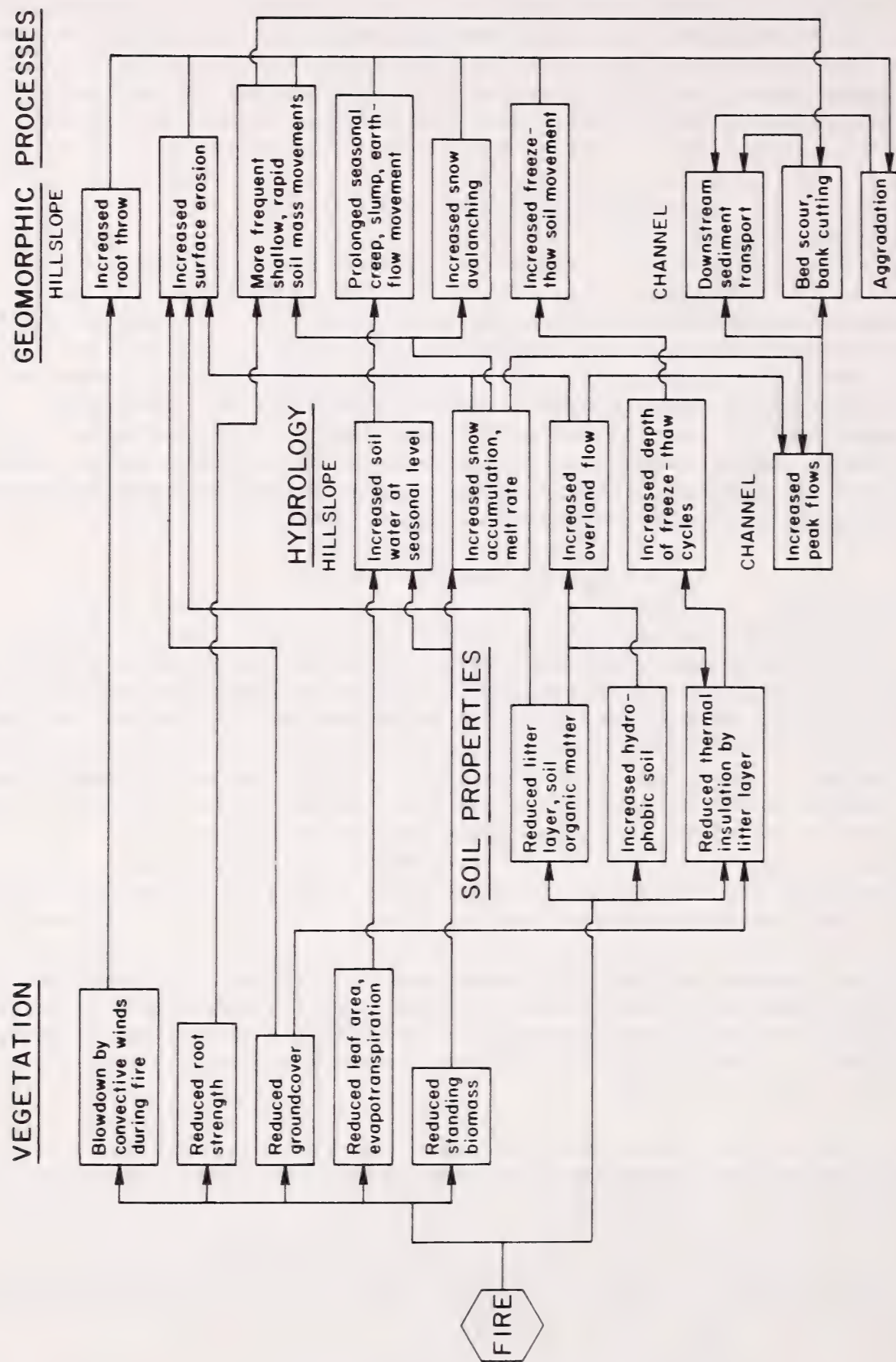


Figure 1.--Effects of fire on vegetation, soil properties, hydrology, and geomorphic processes.

a fire. Fire may have delayed effects on vegetation, as in the case of fire damage to trees which opens the way for attack by insects and decomposer organisms that eventually lead to mortality. As more years elapse before storms and other events trigger change in geomorphic processes, the geomorphic consequences of a fire decrease in response to revegetation. Thus the impact of a fire depends on the timing of major storms. Fire-initiated changes in geomorphic processes may be obvious during the early postfire years, but it is difficult to specify and quantify fire influence in later successional stages.

EFFECTS ON VEGETATION

Alteration of vegetation by fire has several effects on hydrology and geomorphic processes (fig. 1). Fire reduces ground cover of living and dead organic matter and directly causes or initiates mortality and decay of vegetation. Loss of protective organic litter exposes mineral soil, generally increasing its susceptibility to the full spectrum of surface erosion processes. Since a mat of organic matter is also an effective thermal insulator, its removal affects soil temperature regime which is especially important in permafrost terrain. In forest ecosystems, mortality and decay of trees and shrubs leads to reduced rooting strength and increased mass movement potential in steep terrain. Burning of vegetation reduces interception of precipitation and evapotranspiration with resulting increases in soil moisture. The density and distribution of aboveground organic matter also affect snow hydrology, including spatial patterns of accumulation and melt rate.

EFFECTS ON SOIL PROPERTIES

Ahlgren and Ahlgren (1960), Brown and Davis (1973), and others extensively review many effects of fire on soil properties. This review concentrates on soil wettability (hydrophobic tendencies) and thermal effects on frozen ground, because of their important influences on site hydrology which in turn affects geomorphic processes. Combustion of soil organic matter also influences soil properties and geomorphic processes by reducing aggregate stability and thereby increasing susceptibility of soil to surface erosion.

Water repellent soils have been observed in a great variety of ecosystems in dry, unburned soils and soils burned by wildfire and slash fire (DeBano 1969, DeByle 1973, Dyrness 1976, Megahan and Molitor 1975, Campbell and others 1977, and others). Most severe hydrophobic soil conditions are thought to develop in response to fire through litter or slash over dry soils where steep thermal gradients can develop in the soil. Most tests for soil wettability are applied to individual soil particles or aggregates, and hydrologic effects of repellent soils at a broader level are generally unknown. Similarly, the geomorphic consequences of water repellent soil particles are unknown. Increased rill, sheet, and mass movement erosion are commonly observed following intense fire, but the relative importance of repellency, loss of organic matter cover, and other factors in accelerating individual erosion processes have not been determined.

Removal of ground-covering organic matter also affects soil temperature regime, which is particularly significant in soils that experience seasonal freeze-thaw cycles. Hydrologic and geomorphic effects of fire in such systems occur largely in response to alteration of seasonal freeze-thaw cycles (Viereck 1973a, 1973b). Loss of the surface layer of insulating organic matter can result in increased depth and duration of seasonal thawing for a period of at least 15 years following fire (Viereck 1973a). Heat from the fire itself generally has no immediate effect on depth to frozen soil (Brown 1965). Thickening of the active layer may lead to local subsidence, formation of thermokarst, and accelerated solifluction activity in tundra and taiga ecosystems (Viereck 1973a, D. N. Swanston, personal communication). In some vegetation types, vigorous recovery of vegetation over several years results in shrinking of the active layer to a thickness less than prefire conditions (Kryuchkov 1968, in Viereck 1973a).

EFFECTS ON HYDROLOGY

Nonpermafrost terrain also experiences a variety of complex hydrologic responses to fire-induced vegetation and soil changes. In terms of altered ground-water regime, hot ground fire can reduce water storage capacity of surface organic matter (Dyrness and others 1957). Reduced interception and evapotranspiration may result in decreased summer drawdown of soil-water by vegetation (Klock and Helvey 1976a), although in some cases, such as heath vegetation, water loss can be increased when the soil surface is exposed (C. H. Gimingham, Univ. of Aberdeen, personal communication). Effects of reduced interception and evapotranspiration may be offset in part by increased overland flow in response to reduced infiltration due to loss of litter layer, development of hydrophobic soil, compaction by raindrop impact, plugging of pores by fine soil material, and in some instances, actual fusing of soil surface (Dyrness and others 1957; Ahlgren and Ahlgren 1960; Brown 1972; Helvey 1972, 1973; Rice 1973; Anderson and others 1976; Campbell and others 1977; and others). In general, these factors lead to increases in both soil-water storage and runoff from burned sites.

Contrasts in snow hydrology of burned and unburned ecosystems have received very little study, particularly in terms of fire-induced changes in ground-water regime. Snow accumulation and melt in open (clearcuts, natural treeless areas) and forested areas have been the subject of extensive research, but a stand of blackened snags presents a very different environment than either forest or treeless areas. Speculation on snow hydrology of burned areas is complicated by the great contrasts between cold-dry and warm-wet snow types and between snowpack and multiple accumulation-melt seasonal regimes. Work on warm snowpacks by Smith (1974) and others does suggest, however, that formation of melt zones around blackened snags and rapid condensation melting may cause greater melt water input to the soil in burned areas than in forests and snag-free open areas. Forests may have greater loss by evaporation, and snowpacks in open areas may contain continuous, relatively impermeable horizons which carry melt water directly to streams.

These fire-related effects on surface and subsurface hydrology of hillslopes, of course, have direct impact on streamflow. Increased total annual and peak streamflow have been observed from a variety of temperate to semiarid ecosystems involving both snow and rain systems (Rich 1962, Storey and others 1964, Brown 1972, Anderson and others 1976, Helvey and others 1976, Campbell and others 1977, and others). In general, fire-induced changes in streamflow reflect complex interactions among many soil and vegetation factors. Baseflow conditions are most closely related to evapotranspiration and soil-water storage capacity, while peak flows are more controlled by infiltration rate and, possibly, snow hydrology.

EFFECTS ON GEOMORPHIC PROCESSES

Accelerated erosion from burned sites may occur by a variety of surface erosion processes, including dry period ravel, sliding, and surface creep (Anderson and others 1959; Krammes 1960, 1965; Franklin and Rothacher 1962); rill and sheetwash erosion (Sartz 1953, Brown 1972, Rice 1973, Megahan and Molitor 1975, Griffin 1978, Wells and White 1978); wind (Blaisdell 1953, Hinds 1976, Murai and Iwasaki 1976); and cycles of needle-ice formation and melt (Franklin and Rothacher 1962, Wells and White 1978). The relative importance of each of these processes and degree of acceleration due to fire is determined by interactions among soil, topography, vegetation, and climate. Coarser textured soils on steep slopes, for example, are prone to dry-period surface erosion, whereas fine-textured soils are most susceptible to erosion by wind and overland flow processes.

Increased occurrence of shallow, rapid soil mass movement (of debris flow, debris slide, debris avalanche, debris torrent and rapid mudflow types) has also been observed following wildfire (Scott 1971, Rice 1973, Cleveland 1973, Helvey 1973, Klock and Helvey 1976b, Jackson 1977, Scott and Williams 1978). These events are initiated either on hillslopes or in stream channels (Klock and Helvey 1976b). Hillslope events occur in response to rapid rise in ground water level, which may be influenced by fire effects on soil and hydrology, and to reduced rooting strength. The timing of mass movement occurrences following disturbance of vegetation has been explained in terms of root strength variation during the period of root system development by incoming vegetation and decay of dead residual roots of plants killed by clearcutting (Nakano 1971, Swanston 1970, Burroughs and Thomas 1977, and others) and wildfire (Rice 1973). Rapid mass movement events are also initiated in narrow, steep channels when high streamflow entrains large volumes of colluvium along the channel (Anderson and others 1959, Krammes 1965, Scott 1971, Rice 1973, Scott and Williams 1978). Fire affects this process by contributing to increased peak streamflow and by accelerating hillslope erosion processes that supply colluvium to channels between storm events.

Sediment storage in channels also undergoes change in response to fire effects on bedload transport and large organic debris in streams. Increased peak flows may scour and enlarge channels on or close to burn sites (Rich 1962, Griffin 1978). These eroded materials may then be deposited further downstream, aggrading the channel (Rich 1962). Sediment movement and storage in forested streams is also altered when fire increases debris loading, hence channel storage capacity, by causing convective winds that blow trees into channels or triggering downslope log movement. Fire may also decrease debris loading by burning debris in channels and by increasing the potential for channel-flushing mass movement events. Organic debris loading in streams flowing through coniferous forests in the Pacific Northwest may also decrease over about a century following wildfire as residual material from the prefire stand decomposes and is washed away and while the postfire stand develops to the point where it begins to contribute large debris to streams (Swanson and Lienkaemper 1978).

Fire impacts on large, deep-seated (depth to failure surface >2 m) mass movement features such as slumps, earthflows, and zones of deep soil creep are virtually unknown. The greatest potential effects of fire or other types of devegetation involve reduced evapotranspiration and increased soil moisture which could prolong wet season or storm-event related periods of movement (Swanston and Swanson 1976). Effects of rooting strength are trivial in the case of large, deep-seated mass movement features.

The burning of forests on steep slopes at higher elevation may also result in increased snow avalanche activity (Munger 1911, Winterbottom 1974). This occurs in response to reduced effect of vegetation in anchoring snow to slopes and altered snow accumulation and melt patterns in avalanche initiation areas. As a result, unburned forest in the downslope runout area may be battered by snow avalanches. Geomorphic effects of snow avalanches include transport of soil, rock, and organic matter, and uprooting of trees. Repeated snow avalanching and deposition of snow at the end of runout areas suppress revegetation and stabilization of the entire avalanche track area.

The net result of these numerous observed and hypothetical fire effects on individual erosion processes commonly is increased yield of suspended and bedload sediment (reviewed in Wells and others 1978, Rich 1962, Storey and others 1964, Rice 1973, Klock and Helvey 1976b, Campbell and others 1977, Scott and Williams 1978). Increased sediment yield has been reported for watersheds as large as the Trask (370 km^2) and Wilson Rivers (410 km^2) after the multiple, holocaustic Tillamook fires in northwest Oregon (Anderson 1954). In the case of such large fires and long time periods, however, fire effects on sedimentation are confounded by the impact of salvage logging operations and associated roads.

FIRE EFFECTS OVER SEVERAL ROTATIONS

Analysis of Individual Landscape-Ecosystem Types

The overall effect of fire on denudation and sediment yield is best assessed on the intermediate time scale of several fire rotations where both frequency and magnitude of fire-induced periods of accelerated erosion may be examined. Using methods analogous to hydrograph separation, hypothetical patterns of sediment yield are split into components of accelerated sediment yield due to fire and "baseflow" sediment yield rate typical of conditions of well-established vegetation (figure 2). The following examples are from the few areas for which fire regime and related sediment yield data are available.

Perhaps the greatest impact of fire on geomorphic processes occurs in steep land chaparral of southern California where geologically rapid rates of mountain uplift, periods of intense rain, and frequent, intensive wildfire contribute to rapid erosion. Impacts of these factors on rapidly expanding residential development have resulted in extensive study of fire and erosion in this landscape-ecosystem type. Analysis of sediment data from flood-control basins indicates that sediment yield in the first year following fire may be more than 30 times the rate 10 or more years following a fire and that recovery to this "baseflow" rate takes place over 8 to 10 years (Storey and others 1964, Scott and Williams 1978). Fire frequency in chaparral is quite variable, but a frequency of 20 to 30 years is common for many widespread, low elevation southern California chaparral communities (Kilgore 1979).

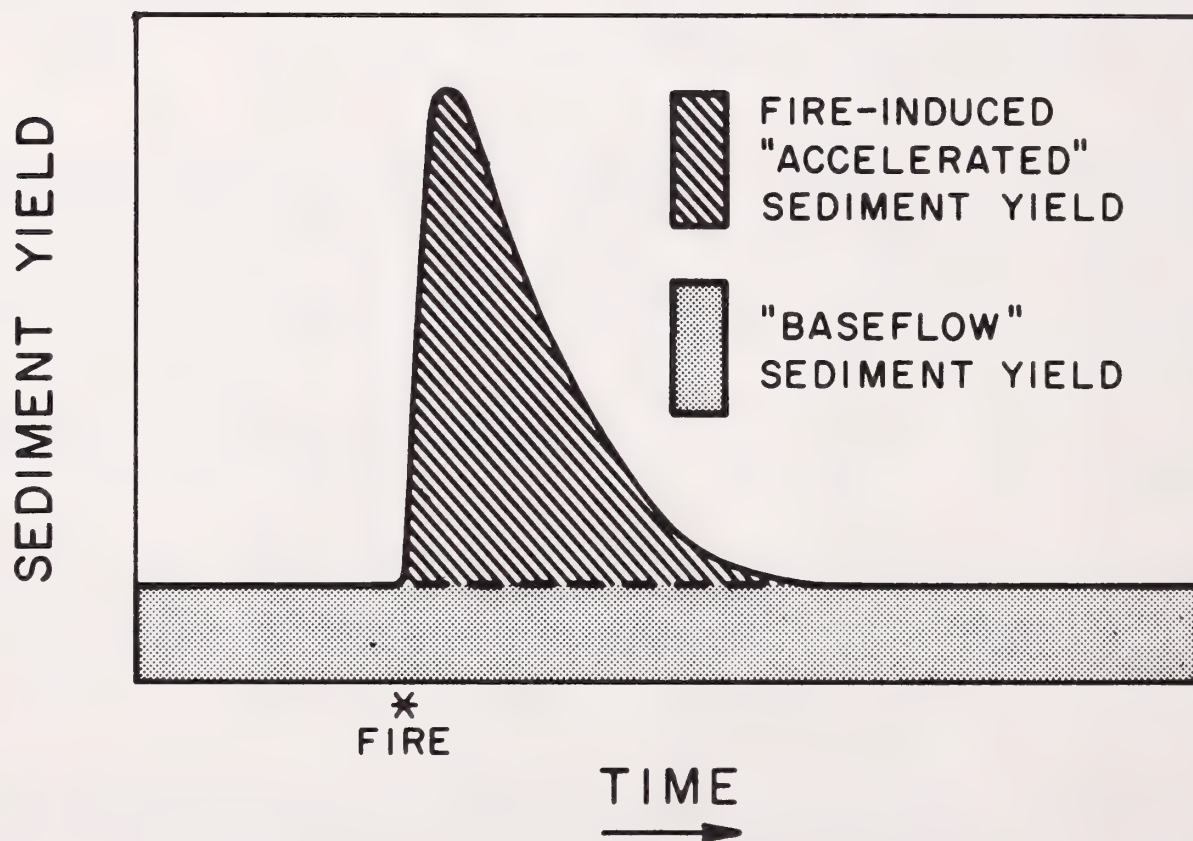


Figure 2.--Hypothetical variation in sediment yield during the period of watershed response to fire. Sediment yield is separated into fire-induced accelerated yield and "baseflow" yield components.

Figure 3A depicts variation in sediment yield from steep, chaparral watersheds assuming a 30-fold increase in sediment yield in the first year following fire, recovery to "baseflow" sediment yield over 10 years, and fire frequency of 25 years. This curve of hypothetical variation in sediment yield is smoothed to remove irregularity due to year-to-year variation in peak flows. Based on integrating the area under this curve and separating fire-induced from "baseflow" sediment yield (fig. 2), fire-accelerated sediment yield totals over 70 percent of total long-term yield from these steep, chaparral watersheds. Rice (1973) has estimated that almost 70 percent of long-term sediment yield from such watersheds occurs in the first year after fire, suggesting an even greater overall fire effect. Results of computer simulation modeling by Bonnicksen (1977) suggest that debris production from a watershed can be ameliorated by managing the frequency of burning and portion of a watershed burned.

The Pseudotsuga menziesii - Tsuga heterophylla forests of western Oregon present another example where accelerated erosion following wildfire is an important, though less dramatic and more poorly documented, contributor to overall sediment yield from small, steep watersheds. Fire regime and related erosion have not been carefully studied in these landscape-ecosystem types, but estimates can be based on reconnaissance studies of fire history and analysis of erosional consequences of clearcutting. These ecosystems experience long return interval, crown fires (Martin and others 1976) at frequencies of 50 to more than 400 years. A 200 year return period may be typical of central western Cascade Mountain forests, although the actual fire regime may involve a longer rotation except for moderate probability of reburn several decades after a fire (Swanson unpubl. data). Following clearcutting and slash burning, erosion by debris avalanches, a dominant erosion process in this steep land, may be increased by about 200 percent over rates measured in forested areas (Swanson and Dyrness 1975). Assuming that other erosion processes are also accelerated, intense wildfire in these steep, unstable terrains may cause a fivefold increase in sediment yield, and recovery to the "baseflow" rate may occur over 20 to 30 years. These estimates of fire frequency and magnitude and duration of accelerated sediment yield are shown as a curve of hypothetical variation in sediment yield in figure 3. Integrating the area under this curve, in the same manner as in the chaparral example, accelerated sediment yield due to fire is about 25 percent of overall sediment yield.

Effect of fire on erosion and sediment yield can also be estimated from studies of varve thickness and charcoal deposition in lakes serving as natural sediment traps. Swain (1973) analyzed the sediment record in a small northeastern Minnesota lake in a mixed conifer-hardwood ecosystem in glaciated terrain of moderate to steep relief. He observed an increase in varve thickness by about 35 percent for approximately 15 years following fire and a fire return period of about 60 years. Under these conditions fire-accelerated erosion contributed a maximum of 8 percent of total long-term sediment yield.

In a Pinus strobus - P. resinosa - hardwood ecosystem and similar landscape in southern Ontario, Cwynar (1978) measured increased varve thickness of about 25 percent for approximately 15 years following fire and an 80-year fire recurrence interval. Based on these estimates, fire-accelerated erosion accounts for up to 6 percent of long-term sediment yield.

Estimates of fire effects on sediment yield using lake sediment records involve uncertainties of not knowing how fire, erosion, and lake sedimentation are coupled and what portions of the basin were burned by individual recorded fires. A more important source of error in these two cases is the predominance of algal gyttia forming the sedimentary record. Much of this material may result from in-lake primary production, and, therefore, does not indicate change in allochthonous inputs.

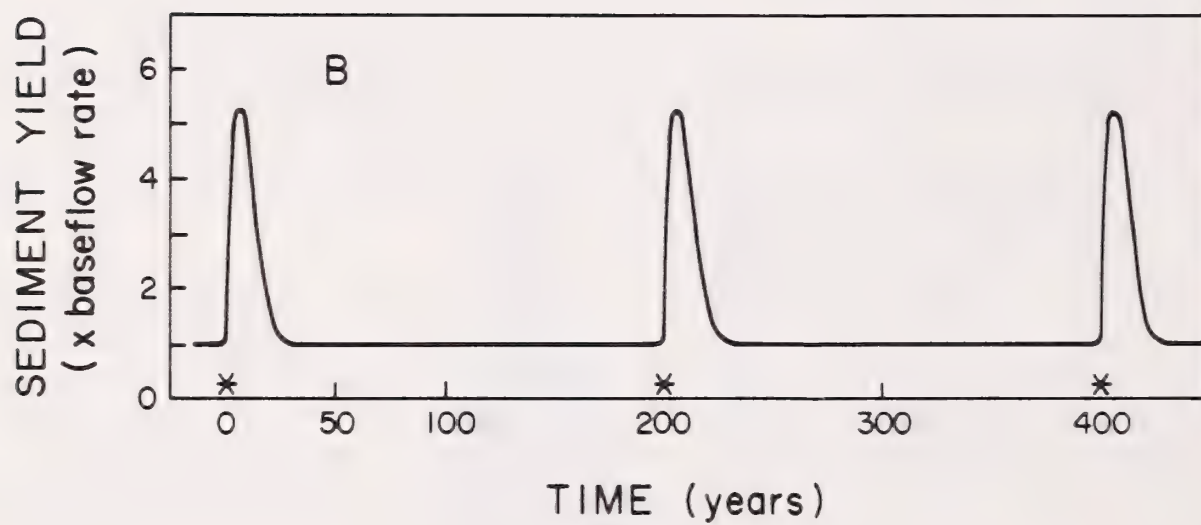
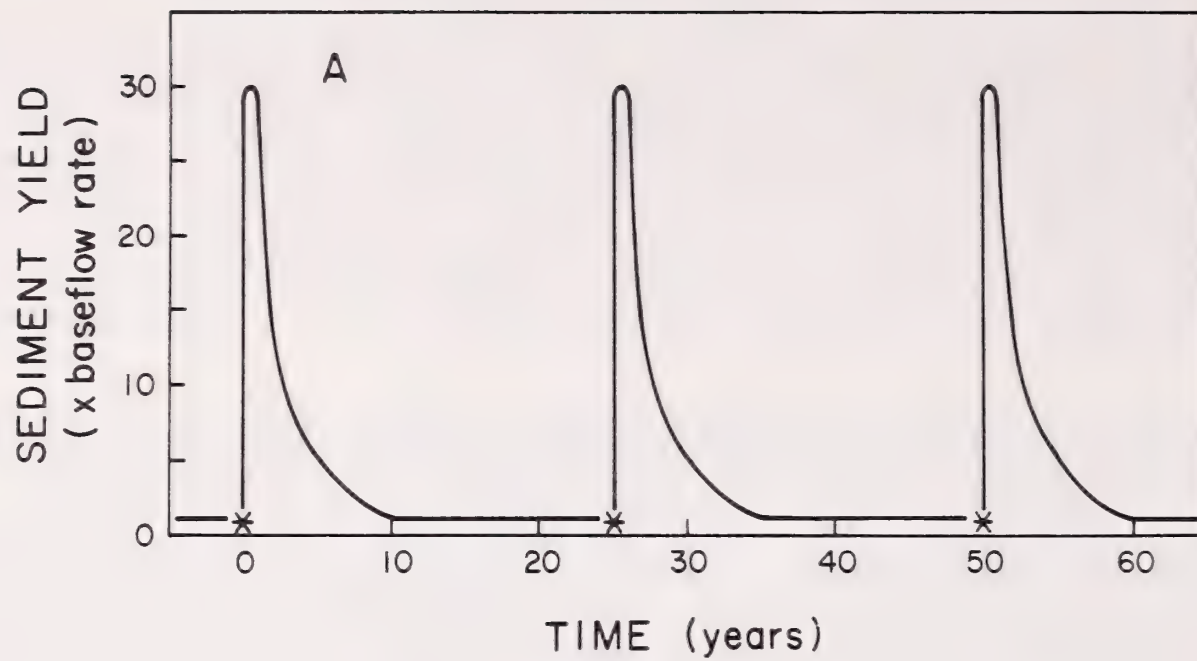


Figure 3.--Hypothetical variation in sediment yield for several fire rotations for a steep-land chaparral system (A) and a *Pseudotsuga menziesii* western Cascade Mountain system (B). * denotes occurrence of fire. Note different scales.

These analyses follow the simplifying assumption that successive fires are independent events occurring at some average frequency longer than the period of recovery to "baseflow" sediment yield. The geomorphic consequences of repeated reburning and related suppression of revegetation due to nutrient depletion and site physical instability have not been examined. Casual observations at sites of repeated intense fire suggest that in portions of these areas recovery of vegetation and the soil-sediment routing system may take centuries.

The strategy for contrasting disturbance-related sediment yield with the "baseflow" yield outlined for chaparral and Pseudotsuga menziesii forests has been proposed as a means of judging impacts of forest management activities relative to the natural fluctuations of the soil-sediment routing system (Swanson and others in press). A key element of this approach is to contrast the frequency, duration, and erosional consequences of natural and man-imposed disturbances of ecosystems. This approach involves a broader time perspective than studies that evaluate management impacts by comparing manipulated experimental areas with undisturbed control areas.

Comparison of Fire Effects in Diverse Landscape-Ecosystem Types

Long-term effectiveness of fire in altering geomorphic processes and sediment yield is best determined on the time scale of several fire rotations. The geomorphic role of fire is determined by (a) fire regime, as defined by Heinselman (1978), and (b) sensitivity of soil-sediment routing systems to disturbance by fire. These two properties are the principal bases for comparing physical consequences of fire in diverse landscape-ecosystem types (fig. 4).

Unfortunately, fire regime and geomorphic and sediment yield consequences of fire are known for very few landscape-ecosystem types. Consequently, figure 4 is proposed as a possible conceptual framework for contrasting fire effects in diverse landscape-ecosystem units. Additional studies of fire regime and associated geomorphology could test and quantify this approach to defining key system property.

Essential elements of fire regime are type (crown or surface), intensity, size, and frequency. Ecosystems with frequent, severe, widespread fires have greatest potential for fire impact on soil-sediment routing. Fire regimes identified by Heinselman (1978) can be roughly ranked by increasing potential impact on geomorphic processes: (Type 0) no (or very little) natural fire; (Type 1) infrequent, light, surface fires; (Type 6) very long interval, crown fire; (Type 2) frequent, light surface fire; (Type 5) long interval, crown fire; (Type 3) infrequent, severe, surface fire; (Type 4) short interval, crown fire. This ranking is somewhat arbitrary, because regimes in many ecosystems involve both crown and surface fire (Heinselman 1978) and the relative geomorphic consequences of these two fire types have not been determined. Geomorphic consequences of a particular fire regime vary with proportions of sprouting plants in burned vegetation, live versus dead fuel consumed, and other ecosystem-specific properties.

To rank ecosystems in terms of fire's potential for impacting geomorphic processes, a more general fire index is used (fig. 4). Fire index increases with increasing fire intensity, frequency, and areal extent.

The sensitivity of a geomorphic system to alteration by fire is largely controlled by hillslope gradient and the effectiveness of vegetation in regulating soil-sediment routing. In landscapes where root strength, ground cover, and other vegetative factors regulate routing, geomorphic processes have high potential for disturbance by fire. This typically occurs in steep, moderately to well-vegetated terrain where surface erosion and mass movement processes are active even under vegetation cover.

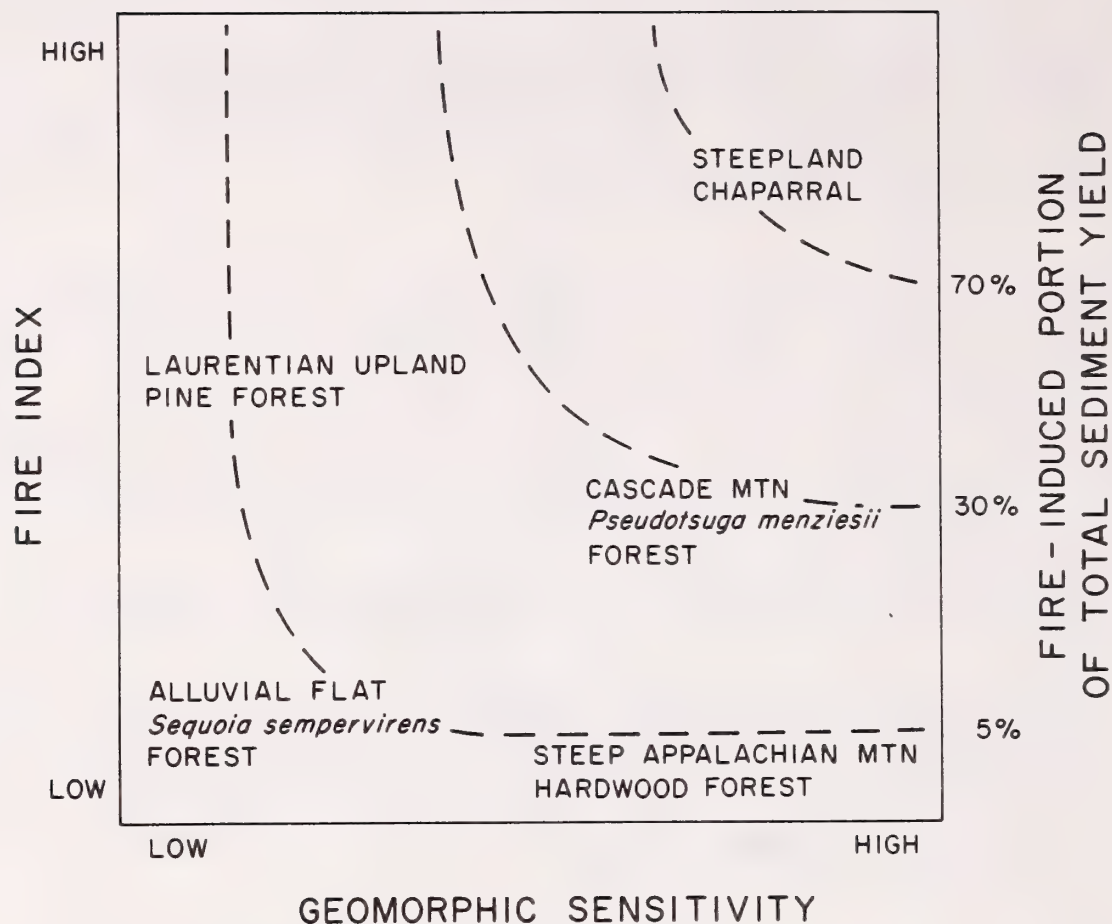


Figure 4.--Hypothetical distribution of selected landscape-ecosystem types with respect to geomorphic sensitivity, fire index (frequency and intensity), and portion of total sediment yield that is fire induced.

Diverse landscape-ecosystem types may be subjectively ordered with respect to fire index and geomorphic sensitivity (fig. 4). Greatest fire impact occurs in the geomorphically sensitive chaparral where short return interval, crown fires may trigger more than 70 percent of long-term sediment yield. Fire is geomorphically less significant in *Pseudotsuga menziesii* forests in unstable Cascade Mountain terrain, largely because of the much longer return interval for fire in this ecosystem. Furthermore, denudation rate of this landscape is only about 5 percent of the rate in the most actively eroding steep, chaparral watersheds in the Transverse Ranges in southern California (Scott and Williams 1978, Swanson, unpubl. data) indicating that the Cascade landscape may be less sensitive to disturbance. These two examples are extreme cases which illustrate geomorphic response to fire that occurs to a more moderate degree in areas of less relief and more stable terrain.

Fire in the boreal and *Pinus strobus* - *P. resinosa* forests of the continental interior Laurentian Upland physiographic province (Heinselman 1973, Swain 1973, Cwynar 1978) is substantially more frequent (60- to 100-year frequency) than in western Cascade *Pseudotsuga menziesii* forests. However, these areas of continental glaciation are topographically subdued, tectonically quiet, and relatively unerodible. Much of the topography has been sculpted by continental glaciation, and nonglacial processes operating over the past 15,000 or so years since glacial retreat have modified the landscape little. Despite moderate frequency, fire has minor geomorphic effect in this landscape-ecosystem, triggering less than 8 percent of long-term sediment yield.

Fire appears to be geomorphically even less significant in the central and northern Appalachian Mountain forests (Wright 1974). Here steep landscapes exhibit moderate to high erosion potential, expressed in part by abundant mass movement activity in response to major storms (Flaccus 1959, Hack and Goodlett 1960, Williams and Guy 1973). Although the natural fire regimes for this area have been obscured by centuries of interference by European man, the wet summer season results in a fire regime of very low frequency and intensity. Consequently, fire plays a very minor role in this landscape-ecosystem type.

In yet other ecosystems fire is virtually nonexistent, limited by low quantities and scattered distribution of fuel in very arid desert ecosystems or by year-round wetness in the cases of tropical forests and coastal Sequoia sempervirens and Picea sitchensis - Tsuga heterophylla forests. These ecosystems occur in landscapes of quite variable erosional sensitivity but, regardless of hydrologic and geomorphic regimes, fire is insignificant, due to climatic factors.

LONG-TERM FIRE-LANDFORM RELATIONS

Relationships between landforms and fire occur as (1) effects of landforms on fire behavior and pattern, and (2) effects of fire on landform development. Long-term interactions among topography, macro- and microclimate, soil, vegetation, and site disturbance factors determine the productivity and community composition of a site, thereby determining local fuel dynamics and fire regime. The distribution of landforms thus has the potential for controlling vegetation patterns on a landscape through its effects on fire.

Aspects of fire behavior such as intensity and rate of spread are regulated in part by topography (Brown and Davis 1973). Faster, more intense burning occurs on steeper slopes due to convective winds and preheating of fuels on the uphill side of a fire front. Steep slopes facing the midday and afternoon sun receive more solar radiation that dries fuels than do flatter slopes or slopes with other aspects. These factors result in faster spreading, more intense fires and higher probability of crowning in forest fires on steeper slopes more oriented to the afternoon sun (Brown 1972). These relations hold only to a certain point, because on slopes over about 40° vegetation and fuels may have a patchy distribution interspersed with exposed bedrock, and these conditions restrict fire spread.

Topography also influences fire pattern by creating firebreaks. Vegetation types that exhibit low fire-carrying capability form subtle firebreaks determined in part by topography and related soil distribution. Completely forested, but sharp, ridges may act as effective firebreaks where upslope mountain winds prevent a fire from crossing. Open water, talus and boulder fields, snow avalanche and landslide tracks, and other barren or sparsely vegetated landscape features form more conspicuous firebreaks. Interesting sets of feedback mechanisms can occur where, for example, fire increases the probability of other disturbance events such as snow avalanches which may create and maintain breaks, thereby restricting the spread of subsequent fires.

Major traditional animal trails may also serve as firebreaks in grassland terrain with little other interruption in topography and fuel continuity. Trails are commonly aligned relative to geomorphic features such as streams, waterholes, and wallows (Clayton 1975, 1976; Babcock 1976). Bison tracks have been recognized as distinctive, though subtle, topographic features in the Great Plains (Clayton 1975, 1976), suggesting that these paths were sufficiently wide, compacted, and poorly vegetated to block grass fires. Tracks of large ungulates in grasslands of the Serengeti Plains, East Africa, mark margins of some grass fires (C. Kucera, personal communication).

The effectiveness of rivers, lakes, wetlands, scarps, and other features as fire-breaks depends on several fire-firebreak relationships. A key consideration is break width relative to the ability of fire to jump or spot over it. Rivers with broad, unvegetated channels, particularly braided channels, are more effective breaks than steeper, smaller streams where less canopy opening and local effects of steep topography may result in complete burning through the stream corridor.

Effects of landforms as firebreaks are more pronounced for low- and moderate-intensity fires. Large, high-intensity forest fires may spread erratically, disregarding slope and spotting long distance over firebreaks (Brown and Davis 1973). These relationships are exhibited in Tande's (1977) stand origin map for the Jasper townsite area, Canadian Rockies where unvegetated river channels are most effective as breaks for smaller forest fires. During years of widespread burning, possibly by multiple large fires, stand age class boundaries are less commonly defined by water courses.

Orientation of breaks with respect to the direction of fire-driving winds is also important in determining the effectiveness of breaks in controlling fire spread (Daubenmire 1936). Elongate breaks will have greatest influence on limiting fire spread where fire burns across the "grain" of topography.

Landforms may affect vegetation pattern on a landscape by contributing to development of plant communities with contrasting fire frequencies or intensities. Vegetation in the lee of breaks may be characterized by older communities with a higher proportion of fire-sensitive species than in less protected sites (Daubenmire 1936, Wells 1965, Grimm, unpubl. cited in Wright, 1979). Firebreaks define boundaries between some major vegetation types, such as the prairie-forest border in Minnesota (Daubenmire 1936, Grimm unpubl. cited in Wright 1979). Based on examples from coniferous forests of the Transverse Ranges, southern California, Minnich (1977) argues that slope steepness and smoothness affect conifer mortality and, thereby, distribution of plant communities. Mapping of fire history in coniferous forests of Mt. Rainier National Park (M. A. Hemstrom, personal communication) and the central Oregon Cascade Range (F. J. Swanson and P. M. Morrison, unpubl. data) reveals an apparent pattern of more frequent fire on upslope areas than along streams. In some areas fires clearly left buffer strips of trees along streams.

Effects of fire on long-term landform development are unknown. Clearly, in some landscape-ecosystem types such as steep-land chaparral, fire has an important influence on rate of erosion and, therefore, rate of landscape development. It is unclear, however, whether altered fire regime and attendant changes in vegetation would affect the type of landforms developed as well as the rate. Key difficulties in identifying the role of fire in landform development are that fire regime is not an isolated variable. Vegetation, soils, microclimate, animal populations and other factors are all interdependent.

On the time scale of broad landform changes all these factors undergo significant natural variation. But on this scale of decades to centuries records are commonly insufficient to determine cause-effect relationships among these variables and to isolate fire effects on gross landform change.

Interpretation of widespread arroyo cutting in the American Southwest between about 1850 and 1920 exemplifies problems in analyzing complex fire-flora-fauna-climate-land use-landform interactions (Cooke and Reeves 1976). Humphrey (1958) and Harris (1966) suggest that reduced fire frequency as a result of suppression by Anglo-Americans allowed encroachment of woody plants into grasslands. Attendant changes in hydrology and soil erosion have been suggested causes of arroyo cutting. However, Hastings and Turner (1965) conclude that fire and fire effects are relatively unimportant in several vegetation zones where arroyo cutting is prominent. In an analysis of 13 factors contributing to arroyo incision, Cooke and Reeves (1976) rank altered fire regime as "probably irrelevant."

In certain favorable circumstances, effects of fire on gross landscape morphology may be less equivocal. For example, such effects might be demonstrable where major valley asymmetry is produced by more rapid erosion from south aspect tributaries which deposit sediment in the main stem, forcing it southward to undercut and steepen northern aspect tributary watersheds (Dohrenwend 1978). If more frequent, intense fire in the south aspect watersheds contributes greatly to higher, long-term sediment yield there, fire is instrumental in shaping gross valley asymmetry. Reduced fire frequency due to suppression or climate change on the scale of millenia might result in a more symmetrical valley cross-profile.

RESEARCH NEEDS

Few, if any, research projects have squarely addressed the problem of identifying and quantifying fire-geomorphic factor relations on both short-term and long-term bases. A summarization of work to date involves compiling information from diverse sources, even for a single area or ecosystem, because there have been no thoroughly integrated studies of fire-vegetation-hydrology-geomorphic process interactions. Such a broad perspective study is underway in southern California Mediterranean ecosystems (Mooney and Conrad 1977).

The key ingredients in such a study are analysis of (a) fire frequency and intensity; (b) patterns of soil and sediment routing through watersheds, including interactions among transfer processes, storage sites, and vegetation; (and c) relations between fire and soil and sediment routing. This information would provide a basis for contrasting the role of fire in different ecosystems and for predicting hydrologic and geomorphic consequences of different fire regimes which would be useful in assessing alternative management practices.

SUMMARY

Interactions among fire, hydrology, and geomorphology vary with the time scale on which a landscape-ecosystem unit is considered. On the short time frame of immediate effects of a single fire on hydrology and geomorphology, fire operates principally through alteration of vegetation and soil properties to alter hydrologic and geomorphic processes. The effects are generally increased soil water and overland flow which result in accelerated erosion by a variety of surface and mass movement processes.

The contribution of fire-induced accelerated erosion to overall sediment yield can be assessed on the intermediate time scale of several fire rotations. At this scale both frequency and magnitude of fire impact may be taken into account. Highly erosive landscapes with frequent, intense fire may have more than 70 percent of their long-term sediment yield exported during the period of accelerated erosion during and immediately following a fire. Most landscape-ecosystem types experience much lower fire impact on soil-sediment routing and sediment yield.

The magnitude of geomorphic effects of fire in an ecosystem depends on (a) the frequency and intensity of fire and (b) the sensitivity of geomorphic systems to disturbance by fire. Geomorphic sensitivity is controlled by hillslope and channel steepness and the effectiveness of vegetation in regulating physical processes in the system. These two properties--fire regime and geomorphic sensitivity--may be used to characterize and contrast geomorphic consequences of fire in diverse landscape-ecosystem types. Frequent, intense fire in highly erosive landscapes, such as steep-land chaparral in southern California, is an extremely important component of some geomorphic systems. Fire is progressively less significant in systems in which fire is less frequent and/or less intense and where erosion potential is lower.

Fire-landform interactions involve topographic effects on fire behavior and pattern and fire effects on landform development. Landforms and associated soil distribution affect vegetation patterning, and vegetation of low fire-carrying capacity forms subtle firebreaks. A variety of hydrologic and geomorphic features function as firebreaks. Long-term fire effects on landform development are uncertain. Fire clearly affects rate of landscape development in fire-prone geomorphically sensitive systems, but whether fire controls the type of landforms developed is unknown.

Clear delineation of fire's effect on physical processes in ecosystems requires analysis of (a) fire frequency and intensity; (b) patterns of soil and sediment routing through watersheds, including interactions among storage sites, transfer processes, and vegetation; and (c) effects of fire on this routing system. Research thoroughly integrating these subjects would increase understanding of ecosystem functioning and provide a basis of evaluating consequences of alternative fire management schemes.

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THE ROLE OF FIRE IN LAND/WATER INTERACTIONS^{1/}

H. E. Wright, Jr.

Regent's Professor of Geology, Ecology, and Botany
University of Minnesota

ABSTRACT

Forest fires cause a temporary increase in runoff to streams and lakes, in part because of decreased evapotranspiration, according to studies in Washington (Entiat Fire), Minnesota (Little Sioux Fire), and Ontario (Experimental Lakes Area). Mass transport of nutrients and cations also increases, but no algal blooms were detected. Extent of fires is commonly limited by natural firebreaks provided by lakes and streams. The charcoal and pollen stratigraphy of annually laminated lake sediments provides a record of past fire frequency. Lake-sediment studies also document forest history over thousands of years, showing the shift from fire-adapted forests to fire-resistant forests, or the reverse.

KEYWORDS: forest fire, nutrients, firebreaks, charcoal, pollen

INTRODUCTION

A major forest fire may be a catastrophic disturbance to a landscape, and one can well suppose that any stream or lake in the area will be seriously affected. It is well established that many of the physical, chemical, and biological characteristics of a lake, for example, directly or indirectly reflect the nature of the vegetation cover in the watershed, and a major perturbation in the vegetation such as fire can be expected to alter the flow of energy and nutrients from one ecosystem to the other (Likens and Bormann 1974). The objective of this paper is to examine various interactions of terrestrial and aquatic ecosystems insofar as they are affected by fire.

The subject can include at least three aspects: (1) effects of fire on the morphology, hydrology, water chemistry, and biological productivity of streams and lakes, (2) the role of streams and lakes in the distribution and severity of fires, and (3) the record of fires contained in lake sediments, both for the historic period

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and for the distant past. The last aspect will be considered in particular, to describe methods by which fire frequency can be determined for the time range beyond the tree-ring record, and to speculate on the nature and magnitude of vegetation changes that may reflect past changes in fire frequency.

EFFECTS ON STREAMS AND LAKES

General

Many mature forests are characterized by (1) a closed canopy that intercepts much of the rain and snow, (2) a deep forest floor that absorbs the moisture and stabilizes the slopes, and (3) a regime of internal cycling that releases only modest quantities of nutrients to streams and lakes, which in turn are adjusted in their chemistry and biology to the stable conditions within the drainage basin. A severe fire in such an ecosystem might be expected to remove much of the canopy, convert the accumulated fuel on the forest floor to readily soluble ash, reduce the infiltration capacity of the mineral soil by developing a water repellency, increase runoff and erosion, and cause algal blooms in streams and lakes by the addition of nutrient-rich water. Several recent studies have been designed to test the various hypotheses involved in these suppositions. A few of these studies will be reviewed, and some generalizations on these and other aspects of the effects of fires on streams and lakes will then be added.

Entiat Fire, Washington

The Entiat Fire in August 1970 in the eastern Cascade Mountains of north-central Washington burned an area of ponderosa pine and Douglas-fir where fire had not occurred for 200 years, and where streamflow had been monitored in connection with another project by the USDA Forest Service for 9 years and water chemistry for 4 months (Helvey 1972, Helvey and others 1976). The immediate effect of the fire was to reduce streamflow for 12 hours, presumably because of direct vaporization of water. Subsequently the diurnal flow variations decreased, as daily evapotranspiration by riverine vegetation was reduced. Water temperature increased as much as 12°C because of the loss of shade. Water yield increased 50 percent during the first year (fig. 1, 2), and the maximum discharge occurred earlier in the spring than usual, as the reduced shade and the blackened surface resulted in faster snowmelt, and as the decreased infiltration of snowmelt into the burned-over forest floor caused increased runoff. In the second year streamflows were even greater (fig. 3), although this increase may be attributed in part to heavy snowpack and very heavy summer rains; severe erosion, landsliding, and siltation occurred, especially in areas where salvage logging had followed fire.

Chemical changes in the streams following the fire have recently been summarized by Tiedemann and others (1978). Three watersheds were burned, but two of them were fertilized with nitrogen compounds and seeded to stabilize slopes and encourage regeneration. Although chemical changes in the three streams were generally similar, the summary that follows concerns only Fox Creek, which was not affected by the fertilizer treatment. The nearby Lake Creek watershed was not touched by the fire and serves as a control.

Alkalinity and conductivity of Fox Creek in one of the burned watersheds were higher immediately after the fire, apparently because of ash washed into the stream, but they returned to prefire levels the next year (Tiedemann and others 1978).

Nitrate-nitrogen concentrations in Fox Creek increased after the fire, and in the second year they were about 6 times that of the control (Lake Creek). The higher values are attributed by Tiedemann and others (1978) first to interruptions of the soil-plant

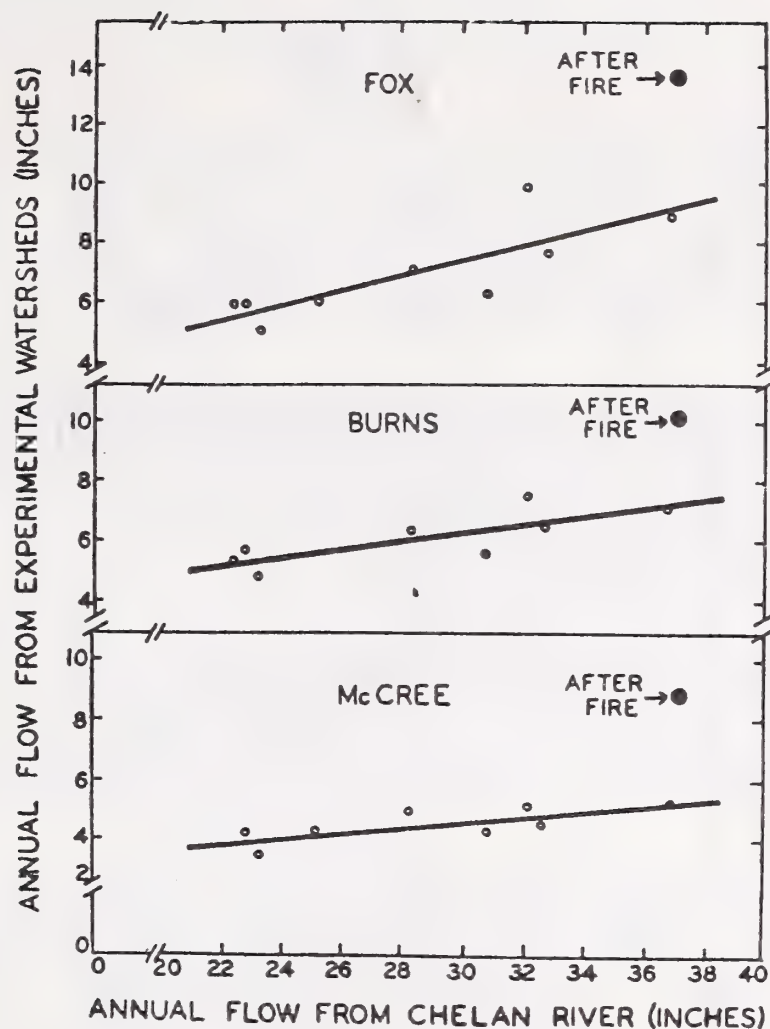


Figure 1.--Annual discharge of three burned watersheds in the Entiat Experimental Forest, Washington, plotted against the discharge of the nearby Chelan River, for the year after the fire as compared to the 9 years of monitoring before the fire. From Helvey (1973, fig. 5).

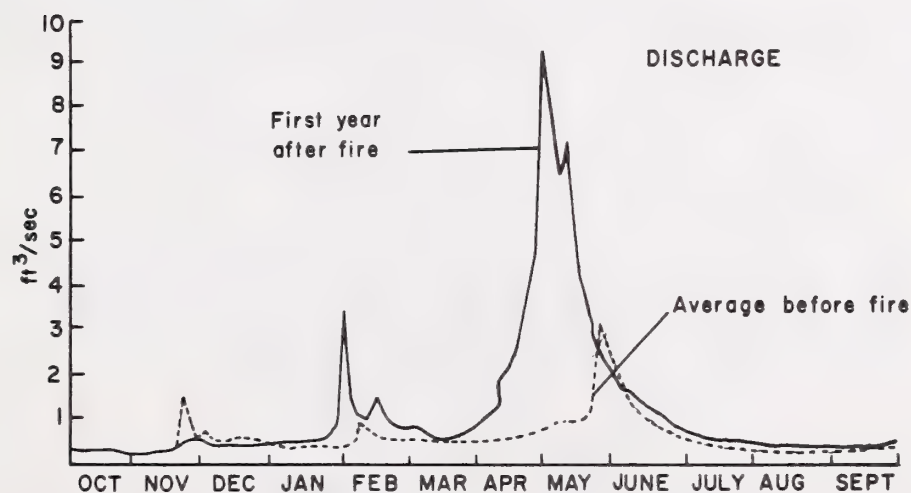


Figure 2.--Discharge of McCree Creek in Entiat Experimental Forest, Washington, for an average year (1962-1963) during the period of calibration, and the discharge for the first year after the fire, which occurred in August 1970 and covered the entire watershed. Extracted from Helvey (1972, fig. 3).

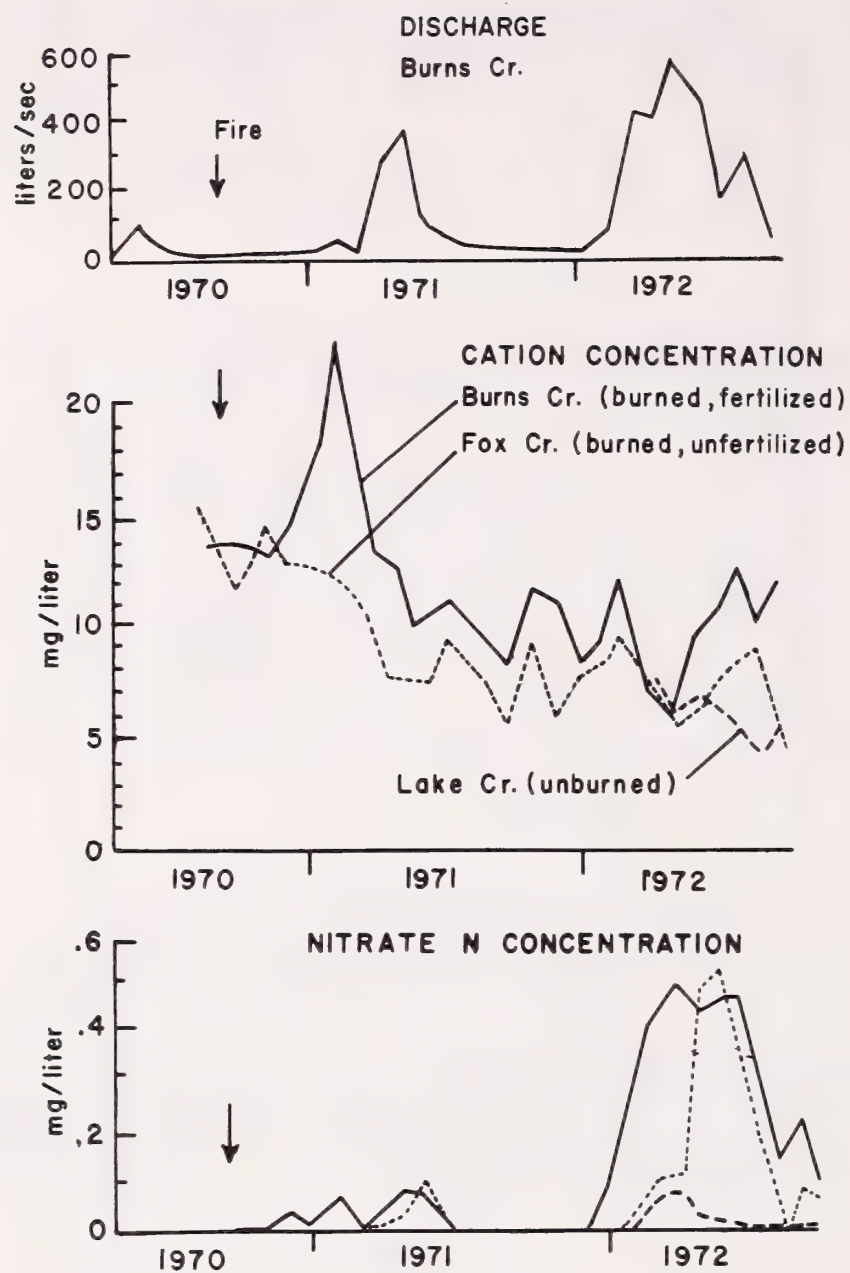


Figure 3.--Discharge for Burns Creek in the Entiat Experimental Forest, Washington, following the fire of 1970, compared with the cation and nitrate-nitrogen concentrations on Burns Creek and Fox Creek for 1971 and 1972 and Lake Creek for 1972. The Burns Creek watershed was fertilized with ammonium sulfate after the fire to encourage the growth of grasses and legumes, but the Fox Creek watershed was untreated; the two streams showed similar patterns of cation and nitrogen concentration. Extracted from Helvey and others (1976, fig. 4-5).

nutrient cycle caused by the reduction of plant growth, and then to increased nitrification caused by higher soil pH. Organic nitrogen concentrations also increased after the fire, as greater surface runoff brought more organic detritus to streams.

Phosphorus was not measured initially, but 2 to 4 years after the fire the concentration of total phosphorus in Fox Creek was 2 to 3 times higher than that in Lake Creek in the unburned watershed. Major cations (Ca, Mg, Na, K) did not increase in concentration after the fire; in fact they decreased, as a reflection of dilution by higher streamflow. Values for Ca were below prefire levels even after 5 years, although the other cations were back to normal.

Concentrations of dissolved nutrients and cations tell only part of the story, however, for stream transport of the solution mass depends as well on stream discharge. Thus the modest increase in nitrate-nitrogen concentrations when coupled with increased discharge in the second year after the fire resulted in a 240-fold increase in solution transport in Fox Creek compared to prefire levels, and a doubling of cation transport (Helvey and others 1976). The loss in total nitrogen during the first 4 years after the fire, however, amounted to only 0.5 percent of the nitrogen capital of the ash and soil. The loss for phosphorus, which is less mobile, was only 0.01 percent, and for calcium 17 percent. Part of the nitrogen loss is made up by precipitation, and much more by nitrogen fixation by Ceanothus shrub, alder, and lupine (Tiedemann and others 1978). Losses of phosphorus and cations must be made up primarily by rock weathering.

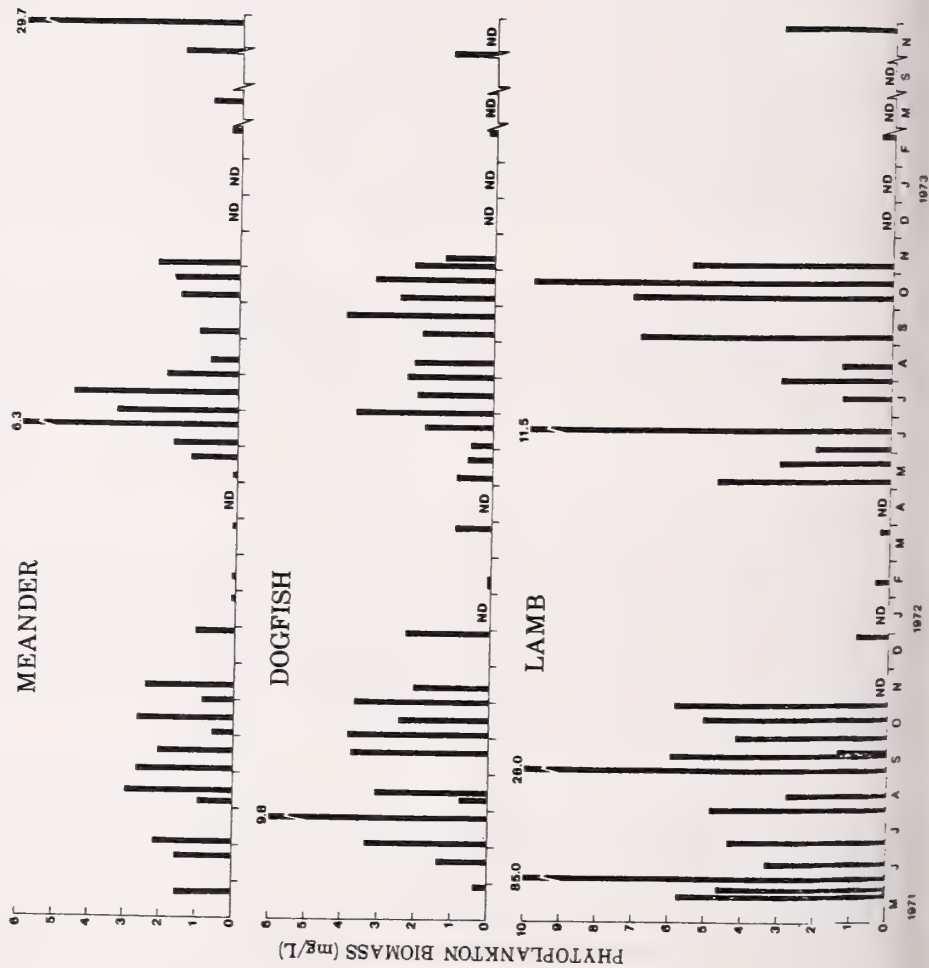
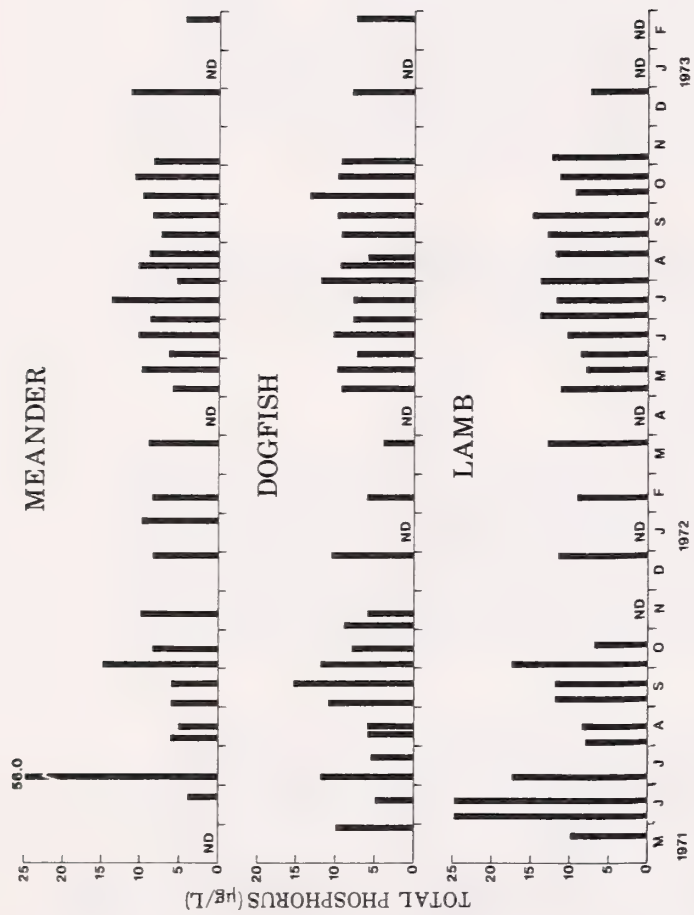
Nitrogen and cation concentrations in streams after the fire were well below limits established by the U.S. Environmental Protection Agency. No measurements of biological activity in the streams were made.

Little Sioux Fire, Minnesota

The Little Sioux Fire in May 1971 in the largely virgin conifer forest of the Boundary Waters Canoe Area of northeastern Minnesota provided the opportunity to examine impacts of wildfire on oligotrophic lakes as well as on the forest itself. Because the fire was unanticipated, the watersheds had not been monitored, so the impacts were assessed by comparing a burned with an unburned watershed of similar size on the same kind of granitic terrain.

Phosphorus released by the burning of living and dead biomass was largely absorbed on the clay components of the soil and then taken up by vigorous vegetative regrowth, which started immediately after the fire (Grigal and McColl 1975, McColl and Grigal 1976). Stream inflow to the lake in the burned area increased by 60 percent compared to that of the unburned area, and this increase accounted for about two-thirds of the 93 percent increase in phosphorus input to the lake from the burned watershed (R. F. Wright 1976) when expressed as phosphorus loading to the lake surface (mg/m^2). This increase is 38 percent, probably within the yearly variation for this forest/lake ecosystem, in which most of the phosphorus input comes ultimately from precipitation rather than from rock weathering. As was the case with the Entiat Fire in Washington, the loss of phosphorus from the watershed was small compared to the phosphorus capital of the forest/soil system. Analysis of the total phosphorus, phytoplankton biomass, and chlorophyll a concentrations (fig. 4) made at generally biweekly intervals for 2 years after the fire showed no significant increase attributable to the fire, nor any differences in the composition of the phytoplankton (Bradbury and others 1975, Tarapchak and others 1979).

Of the cations, calcium export from the burned watershed increased 26 percent compared to the unburned, magnesium 29 percent, sodium 65 percent, and potassium 265 percent. Most of the cations were flushed out the lake outlet. Only potassium is important biologically in the lake, but it is already present in such a large quantity that it does not effect algal growth, and its increase after fire had no impact on the lake ecosystem.



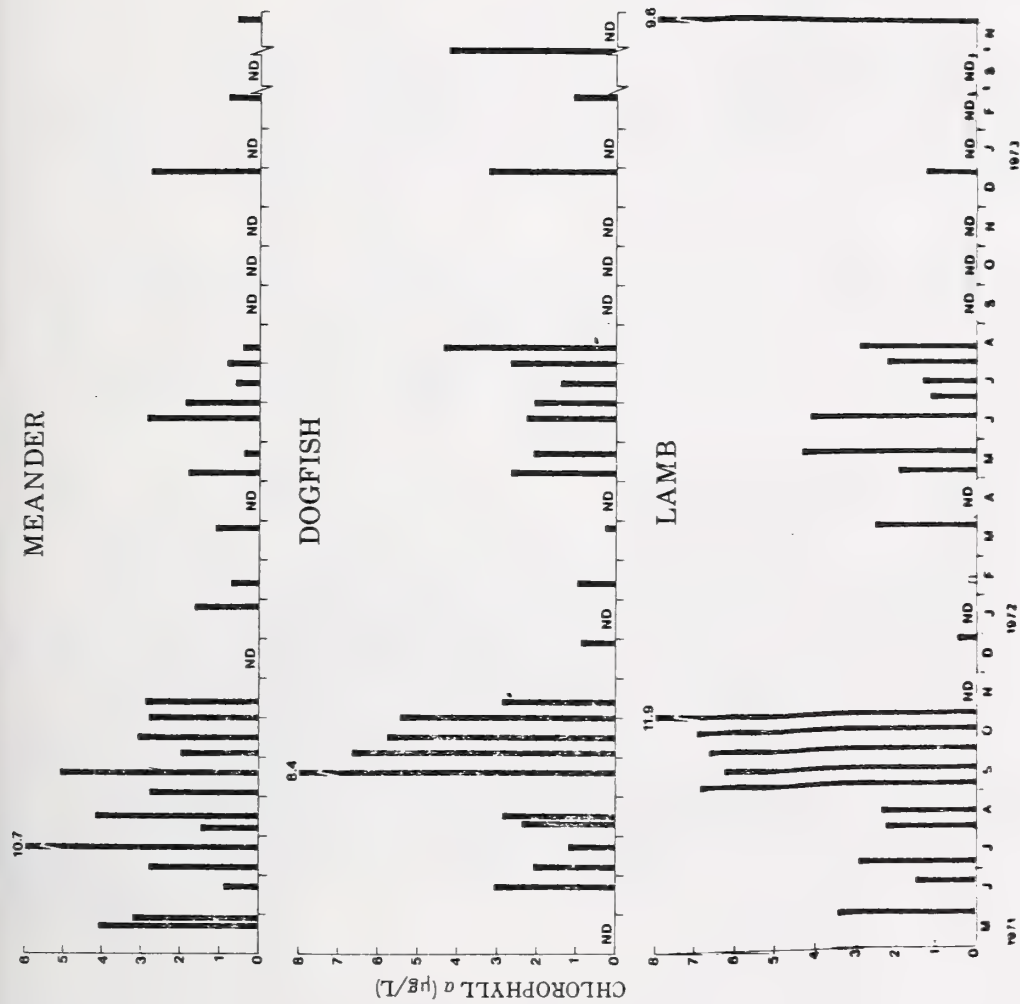


Figure 4.--Total phosphorus, phytoplankton biomass, and chlorophyll a for generally biweekly water samples from Meander and Lamb Lakes (burned watersheds) and Dogfish Lake (unburned control), Minnesota. The fire occurred in May 1971. ND means no data. From Tarapchak and others (1979).

ELA Fire, Ontario

An even better test of the effects of forest fire on lakes was made possible by events in the Experimental Lakes Area in northwestern Ontario (Schindler and others 1979). Here two watersheds monitored for 4 years were subject to a violent windstorm in 1973 and then a year later in 1974 by a summer wildfire, followed by drought with little vegetative regrowth and then by two major rainstorms. An adjacent monitored watershed was untouched by winds or fire, providing exceptional circumstances for assessing nutrient release after fire.

Water yields from the blowdown (both during storms and during base flow) increased immediately, and they further increased after the fire, but in the third year the vigorous vegetative regrowth renewed the evapotranspiration losses from the forest, and the runoff decreased to normal levels.

Nitrogen concentrations increased only slightly after both windstorm and fire. Because of the greater runoff, the total nitrogen loss from these watersheds about doubled. Phosphorus concentrations were not affected by the windstorm but increased after the fire; total loss was greater in all years. For potassium, both concentrations and yields were increased in all cases.

Because precipitation accounts for most of the nutrient input to this forest ecosystem, the perturbations brought by windstorm and fire have little effect on the long-range nutrient supply to the forest nor to the runoff streams. No increases in nutrient or phytoplankton concentrations were noted in a lake into which the monitored streams drained.

Miscellaneous Studies

A variety of physical and geological effects of fire on different time scales are covered in a companion paper in this volume by Swanson and some additional biological aspects by Tiedemann. Quantitative analysis of stream discharge and sediment production during 7 years of recovery in the burned watersheds of the Entiat Fire, newly discussed by Helvey (1979), show that peak discharges during snowmelt have decreased in successive years as leaf litter builds up and improves soil infiltration, and as evapotranspiration from the developing canopy takes up some of the excess. Concomitantly sediment production has lessened as the supply of eroded material from revegetated hillslope diminishes and as the stream channels themselves become stabilized. But it is anticipated that stream discharge and sediment production will not return to prefire levels for several decades.

All of these studies show that mountainous regions are much more susceptible to various kinds of erosion after fire than are the interior plains. Degradational processes such as particle creep, slump, washouts, earthflows, and mudflows are all enhanced by steep slopes and thin soils. These in turn may result in local sedimentation along streams, destroying certain habitats for aquatic organisms but creating others. Between fires, dead trees on the lower slopes fall into streams, producing debris dams that may eventually get flushed out by occasional torrents, or burned out in the next fire (Swanson and Lienkaemper 1978). Thus the macrobiology of mountain streams may be indirectly controlled by fire frequency. But the wildfire studies reviewed above indicate that nutrient supply to streams and lakes apparently does not change enough to affect the microflora.

FIRE AT THE PRAIRIE/FOREST BORDER

A different interrelation of fire and water can be seen in the transition from prairie to forest--but here it is not the fires that affect the water bodies but the reverse.

Since the work of Daubenmire (1936) in the "Big Woods" of south-central Minnesota, it has been recognized that the natural position and composition of the prairie/forest border was determined in part by the incidence of fires that originated in the prairie and swept into the forest margin, killing or preventing the establishment of the fire-intolerant trees and favoring the thick-barked bur oak and certain trees that sprout readily if damaged. Tree relations today are not easy to see in the field, however, not only because agricultural clearance has opened the forest extensively in the transitional area, but also because fire protection has permitted the forest to advance into the prairie.

Examination of the land-survey records that were made before significant agricultural development in the area reveals the natural distribution of forest and prairie, as well as the species composition of the forest. The records contain the identification of two or four "witness trees" at every half mile along the surveyed section lines, thus as many as 288 trees for each township (36 square miles). A compilation of the data in a current study by Grimm (1979) for the entire Big Woods area, which measures about 160 x 100 km, shows not only that the position of the prairie/forest border is controlled in detail by such firebreaks as streams and lakes, but that the composition of the forest can also be related to this factor (fig. 5). Thus bur oak and aspen were dominant at the prairie border in the more exposed areas where fire frequently invaded the forest, for bur oak has thick bark, and aspen readily sprouts after fires. Elm, basswood, ironwood, red oak, and particularly sugar maple, on the other hand, are susceptible to fire and were confined to areas in the lee of firebreaks or in morainic topography where the spread of fire is interrupted by valleys.

Stratigraphic pollen analysis by Grimm of lake sediments in the area implies that the forest moved slowly westward for several thousand years to its present position, although enclaves of forest occupied areas in the lee of lakes and in rugged topography during earlier times when the climate was drier and prairie was more extensive. Oak and possibly aspen invaded prairie and dominated the arboreal vegetation until only a few hundred years ago, when the populations of the fire-intolerant trees characteristic of the Big Woods greatly increased, probably because of climatic cooling correlated with the "Little Ice Age." The forest invasion of prairie occurred at different times in different places depending on location--first in areas protected by firebreaks and in strongly rolling topography, and later in flatter land and in areas farther west. There is some indication that the migration and expansion took place in steps, from one firebreak to another. In any case it seems clear that water bodies have played a significant role in the composition of the forest.

The effectiveness of lakes as firebreaks in the northern conifer forest can be seen in the Boundary Waters Canoe Area in northeastern Minnesota, where more than 1,000 lakes dot the million-acre wilderness area. The relations are apparent on the stand-origin maps of Heinselman (1973), which reflect the ages of fire-adapted units in the forest mosaic and thus serve to show the areal extent of past fires. Many of the units terminate on the south or west shores of large lakes and streams, and it is clear that although fires occasionally jump ahead over water bodies their limits are commonly determined by such firebreaks, and the oldest stands of trees are commonly found on islands or peninsulas that have escaped fire for several centuries. The relations could be quantified by plotting the ratio of lakeside or streamside perimeter of a fire to total perimeter. Orientation of firebreaks could then be examined and inferences made about wind directions at the time of fires.

In the western mountains, stream valleys also serve as firebreaks, especially broad valleys with wet meadows on the valley floor. In steeper mountain topography, however, a fire can often spot from one side of a valley to another; here ridge crests are more commonly firebreaks than valley bottoms, because air convection usually accentuates the upslope progress of fire when aided by the wind. If maps of past fires are prepared, directions of fire winds might be worked out from the orientation of the ridge crests that served as firebreaks.

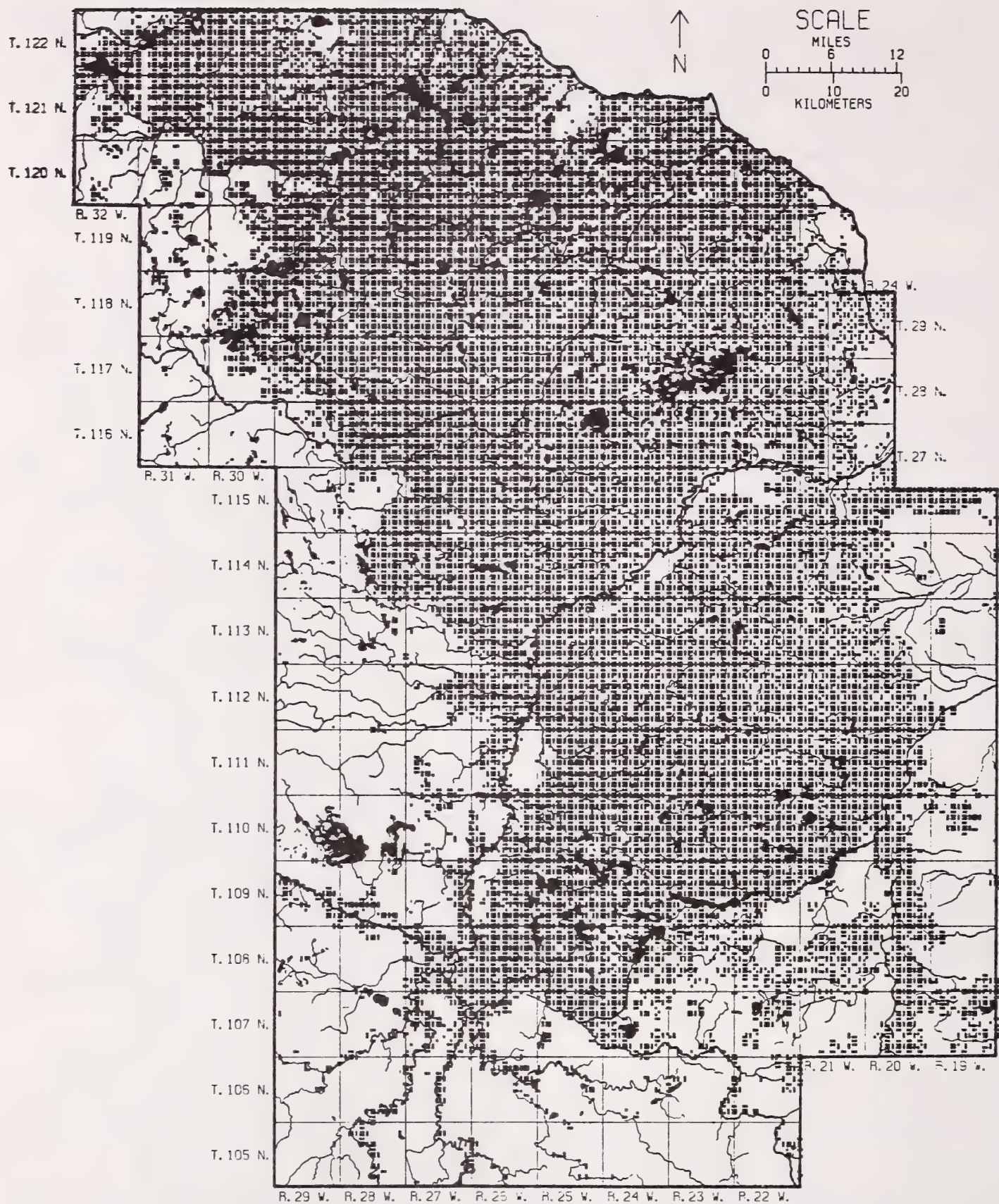


Figure 5.--Distribution of trees in the Big Woods of south-central Minnesota, plotted from the land-survey records prior to agricultural land clearance. Note that the prairie/forest border coincides in many areas with streams and lakes. From Grimm (1979).

The third approach to fire/water interactions involves the fact that lake sediments offer the opportunity to study the incidence of fire in the distant past, to cover the time range before the period accessible by tree-ring analysis in extant forests. In certain respects a lake can be viewed as a passive recorder of events in a forest/lake ecosystem, for much of the sediment it receives from its drainage basin or generates by its own productivity settles to the bottom and is progressively buried. The sedimentary record is particularly useful if it features annual laminations, for these provide the means for a precise chronology as well as the indication that the bottom deposits are absolutely undisturbed by burrowing organisms or by deep water currents.

The most direct evidence for fire that can be determined from lake-sediment study is the stratigraphy of charcoal fragments, which are deposited as airborne ash or are washed into a lake from burned hill slopes. The first such detailed study made was that of Swain (1973) at Lake of the Clouds in the conifer forest of north-eastern Minnesota, where the importance of fire as a major factor in forest composition is documented for the last 350 years by the tree-ring and fire-scar studies of Heinselman (1973). Lake of the Clouds contains annually laminated sediments (Anthony 1976), which provide the opportunity for precise dating of stratigraphic changes in charcoal and other sedimentary components, as well as the determination of the sedimentation rate as it might be affected by postfire events. The charcoal and pollen content were analyzed at 2-year intervals for sediment deposited from 1890 to 1970 (Swain 1979) and at 10 to 20 year intervals for the last 1,000 years (Swain 1973). Results reveal variations that can be correlated with the tree-ring fire chronology for the past 300 years, and additional variations during earlier centuries suggest an average fire-recurrence interval for the area of about 65 years for the past 1,000 years (fig. 6). Stratigraphic changes of significance include a maximum in charcoal abundance and particularly in the ratio of charcoal to pollen grains, a decrease in the pollen ratio of conifers to "sprouters," and a slight increase in thickness of annual laminations. The charcoal stratigraphy is not so sharp as one might hope, probably because of continued inwash of charcoal fragments from hillslopes for several years after a fire, or because of redeposition from shallow to deep water at times of lake turnover. The increase in pollen percentage of "sprouters" (birch, aspen, alder, hazel, bracken, and grasses) is attributed to the growth of these plants in the sunlight after removal of the canopy by fire, as well as to the delay in the maturation of pine seedlings (usually at least 10 years in the case of jack pine, longer for red and white pine). The increase in thickness of laminae after inferred fires is attributed to algal productivity resulting from nutrient influx, although other factors may be more important, such as increase in sediment focusing in the deep part of the lake after the forest canopy is removed by fire, allowing winds to generate stronger water currents.

A similar stratigraphic study of annually laminated lake sediments was made by Swain (1978) at Hell's Kitchen Lake in northern Wisconsin. In this case fire frequency is best reflected by maxima in birch pollen, averaging about 120 years apart for the interval 200 to 300 years ago. White pine pollen increased 40 to 80 years after most of the birch pollen maxima, and hemlock increased 80 to 170 years after birch, as these conifers succeeded birch and aspen during intervals between fires. Average return interval between fires is estimated as about 140 years through the last 1,150 years, and 100 years before that. Relatively moist climatic intervals are inferred from higher pollen percentages of white pine and/or hemlock relative to oak and aspen, and from greater ratios of yellow birch to paper birch seeds. During these moist intervals the charcoal abundance is less than during the inferred dry intervals.

LAKE OF THE CLOUDS, MINNESOTA

A. M. Swain 1973

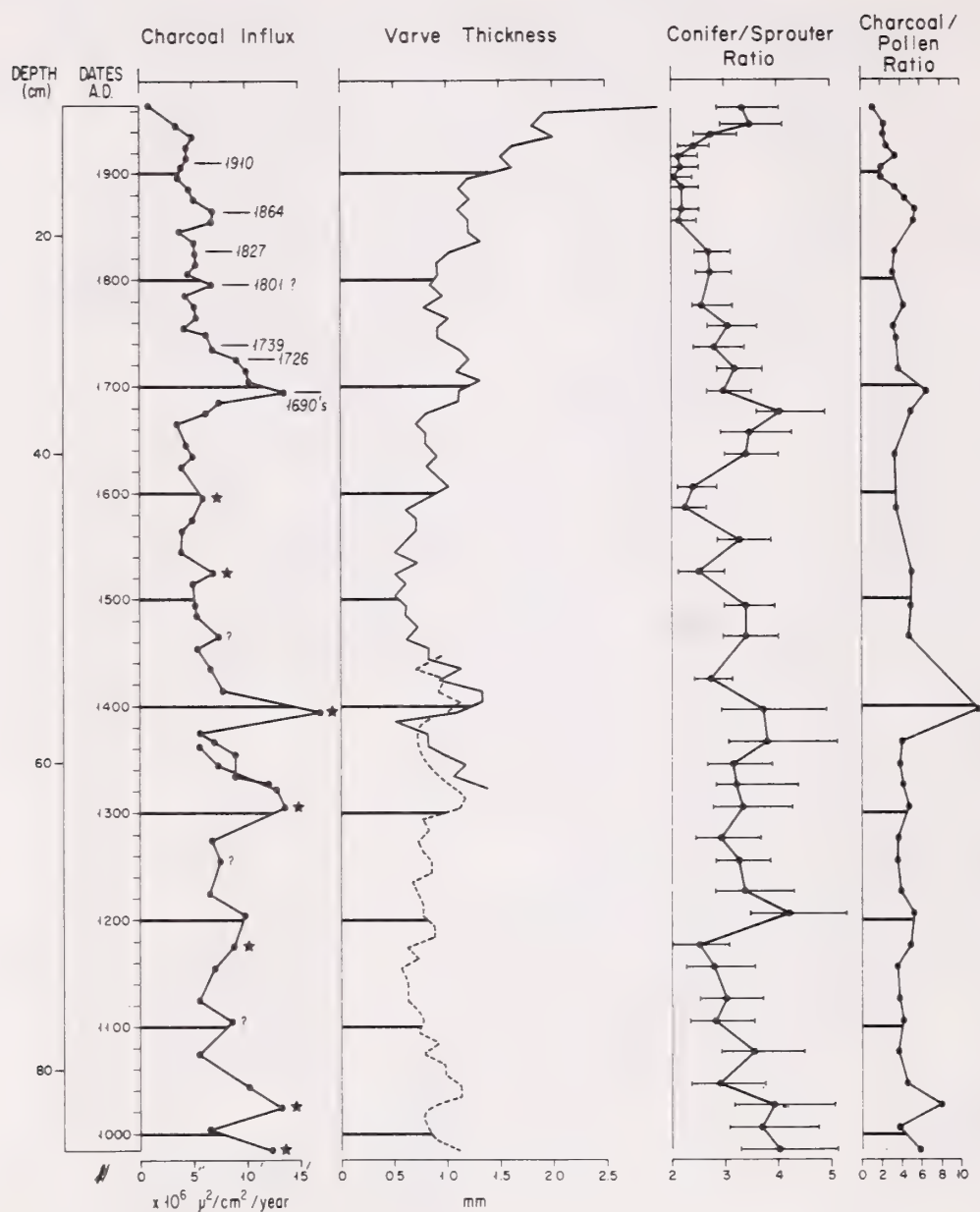


Figure 6.--Stratigraphic profiles from a short core of annually laminated (varved) sediments from Lake of the Clouds, north-eastern Minnesota, showing how several maxima in the influx of charcoal match the dates of fires as known from tree-ring studies back to the 1690's. Before that, important charcoal maxima (starred) match the maxima in varve thickness and charcoal/pollen ratio of trees and shrubs that sprout after fires. Extracted from Swain (1973, fig. 3).

The only other area in the western Great Lakes region where a sizable stand of old-growth pines permits the technique of charcoal stratigraphy to be checked against a tree-ring chronology is in Itasca State Park in northwestern Minnesota (Frisell 1973). The advisability of close-interval sampling of annually laminated sediments is seen from a study by Foster (1976) at Lower LaSalle Lake in this area. The pronounced charcoal stratigraphy can be correlated easily with the incidence of known fires (fig. 7). The most prominent fires in the area, as well as in the rest of Minnesota and perhaps western North America as well (Heinselman 1979), were in 1863-1864, and this shows as a major maximum on the profiles. Another big year for fires in the Itasca area was 1874. The highest peak on the curve for total charcoal, at 1895-1900, reflects slash burning in the area associated with the period of most extensive logging. The peak at about 1935 registers fires during the drought years of the 1930's.

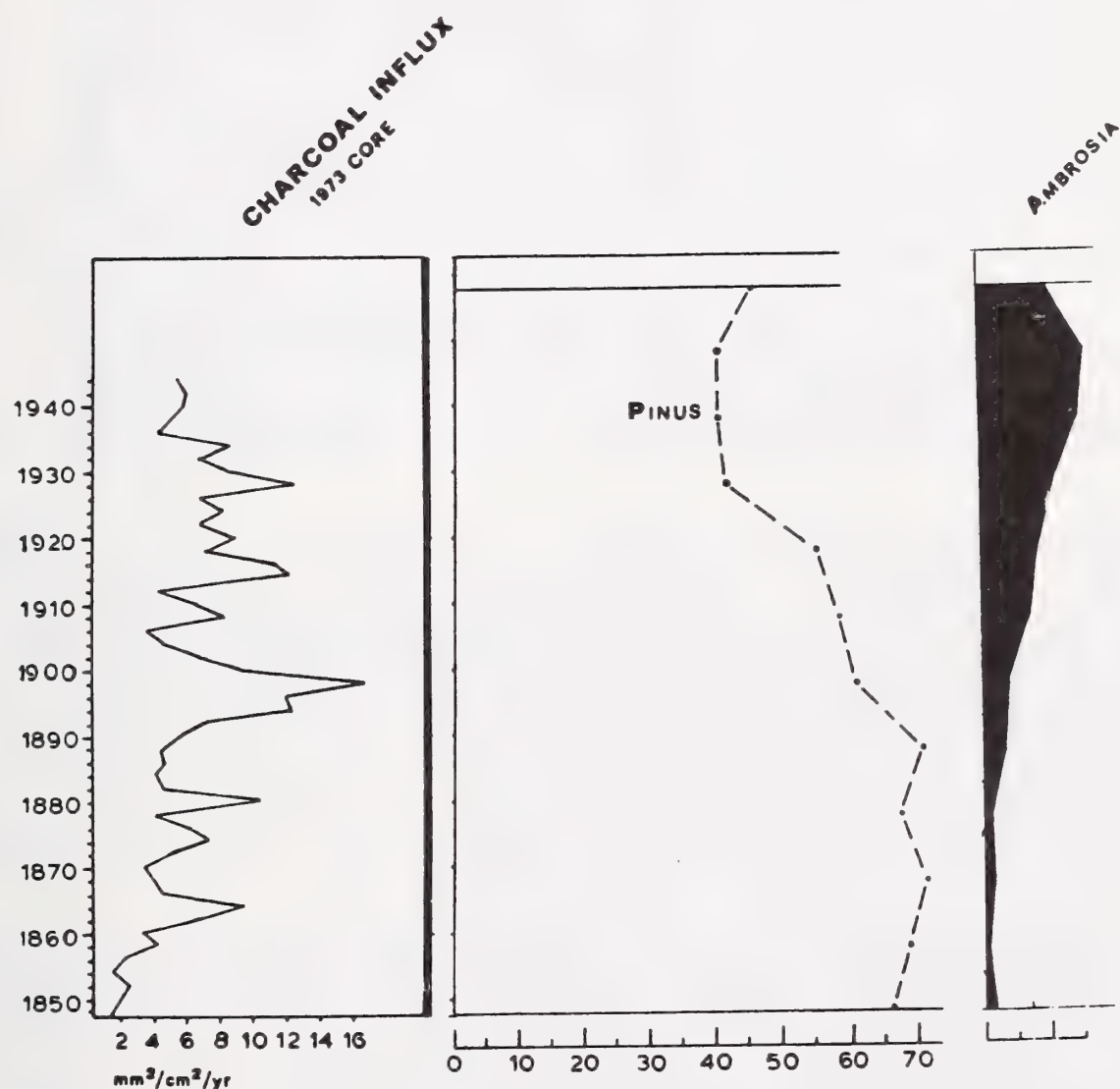


Figure 7.--Charcoal stratigraphy for the interval 1844-1944 from annually laminated sediments at Lower LaSalle Lake near Itasca State Park, northwestern Minnesota, compared with the decrease in pine pollen related to timber cutting and the increase in pollen of Ambrosia (ragweed) attributable to agricultural and land clearance. The charcoal maxima correlate with fires known from the tree-ring record. From Foster (1976).

This and the other stratigraphic studies of laminated lake sediments so far described were made on frozen cores, acquired by dropping a weighted metal tube filled with dry ice and butanol into the sediment. If left in position for about 30 minutes a crust of sediment a centimeter or so thick will freeze to the outside of the tube. When withdrawn to the surface the crust can be closely sampled, with careful avoidance of the thin distorted portion immediately next to the tube.

Another stratigraphic project in the Itasca area was undertaken at Squaw Lake by Patterson (1978), who combined this stratigraphic approach with a 2-year study of the hydrology and water chemistry of the lake and its influent streams. The watershed consisted primarily of birch and aspen regrown after largely clearcut logging of pines, followed by slash fires. During the period of observation a very heavy rainfall resulted in conspicuous stream erosion and inflow of mineral sediment to the lake, producing a thin layer of white silt in the otherwise organic sediments. A core of sediments from the deepest part of the lake showed several such silt layers, many of which occur just below maxima in the charcoal profile (fig. 8). Patterson concludes that periodic deforestation by fire resulted in erosion of the forest floor at the time of the next heavy rain, with the mineral sediment settling out in the lake more rapidly than the more buoyant charcoal particles. Although the lake sediment is not annually laminated, the sedimentation rate could be determined by identification of the level of the rise of ragweed pollen and the decrease in pine pollen, marking the time of farming in areas to the west and logging in the Itasca area itself. A radio-carbon date near the base of the section provides an additional datum. The extremely low sedimentation rate--only about 6 cm per century, unusually slow for a Minnesota lake--as well as the irregularities introduced by the silt bands, make it difficult to correlate closely the charcoal stratigraphy with the tree-ring record of past fires.

Another study in which fire-induced erosion is inferred from the stratigraphy of annually laminated lake sediments is that of Cwynar (1978) at Greenleaf Lake in Algonquin Provincial Park west of Ottawa in forest of dominantly white pine. He found that maxima in charcoal profiles (fig. 9) correlate with thick annual layers and with high influx of pollen, aluminum, and vanadium, presumably because of enhanced erosion following fire: the pollen was washed into the lake from the forest floor, and the mineral ions were contributed by soil erosion. Analysis of 10-year samples through a 500-year section of sediment dating from 770 to 1270 A.D. yielded a fire frequency of about 80 years. Pollen analysis indicates that regional forest composition did not change during this period or in subsequent time.

A different sedimentary approach to fire history was applied by Griffin and Goldberg (1975) to the annually laminated sediments of the Santa Barbara basin off the coast of southern California and Saanich Inlet in British Columbia. Here the technique involved the determination of elemental carbon, which ranged from 0.01 to .09 percent of dry weight. Results show a slight increase over the last 120 to 135 years, although the scatter of points is very large. The authors believe that the carbon is derived from fires in chaparral or forest, either by smoke or by subsequent erosion of burned landscape by streams, even though they list several other possible factors (burning of fossil fuels, microbial decomposition of organic matter, variations in winds and streams). Although they show by scanning electron micrographs that the carbon particles resemble those derived from burned wood, they state that fossil fuels could produce similar particles. Their conclusion that "management practices in the control of forest and brush fires of California and British Columbia appear to have had little effect on the fluxes of elemental carbon in the marine environment" would seem to be unwarranted, in view of the uncertainties in the source of carbon and in the mode of transport of the site.

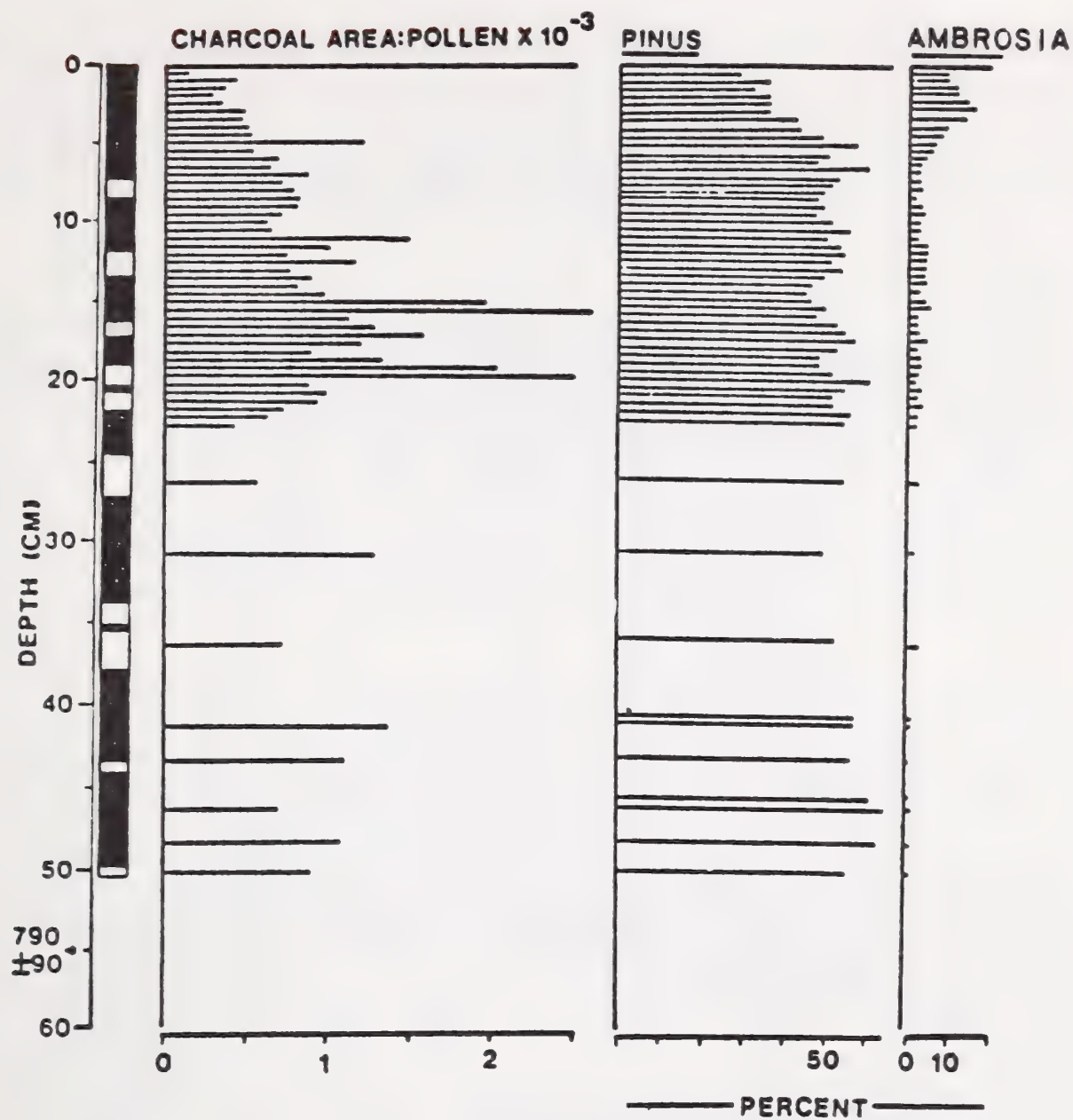


Figure 8.--Charcoal stratigraphy for a short core from Squaw Lake in Itasca State Park, northwestern Minnesota. Time scale is provided by a radiocarbon date at 55 cm and by the rise in ragweed pollen and fall of pine pollen, dated to about 1895 on historical evidence. Maxima in the charcoal curve down to a depth of 16 cm correlate with fires from the region as known from the tree-ring record. Several charcoal maxima occur just above the bands of silt (white on sediment column), which may represent erosion after fire. From Patterson (1978).

GREENLEAF LAKE, ONTARIO

Algonquin Park

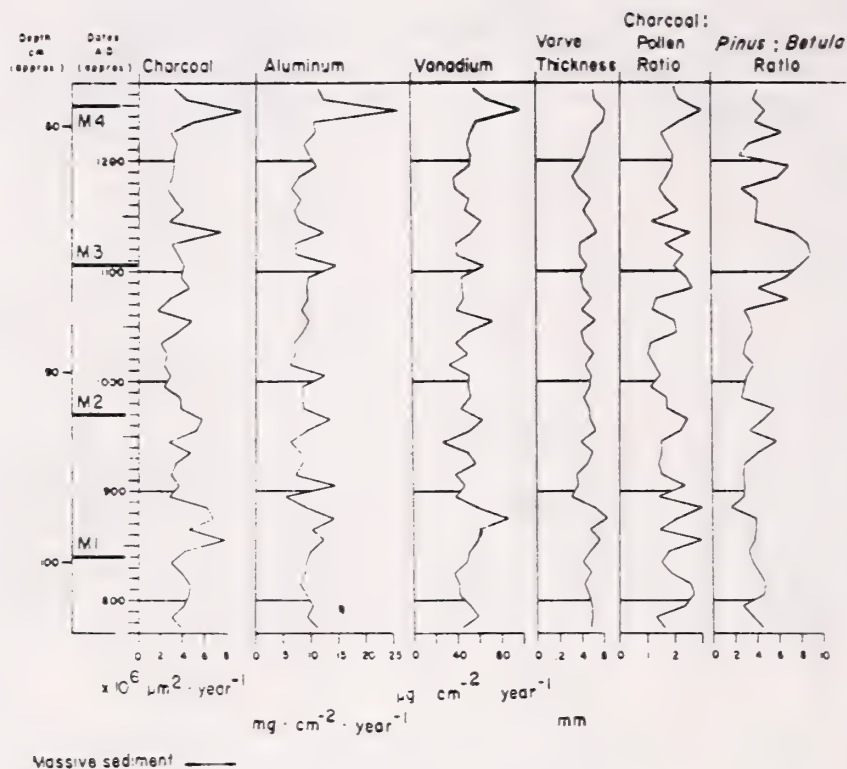


Figure 9.--Stratigraphic profiles for charcoal and other components in the annually laminated sediment from Greenleaf Lake, Adirondack Park, Ontario, for the time interval 770-1270 A.D. Massive layers M-1 to M-4 are interpreted as turbidities. Charcoal maxima correlate with maxima of Al, Va, and lamina thickness, implying hillslope erosion after fire. Extracted from Cwynar (1978).

A more realistic analysis of the Santa Barbara varved sediment was made by Byrne and others (1977), who were able to correlate the influx of charcoal particles in core segment 1931-1970 with the known years of wildfires in the Los Padres National Forest on the mainland only 25 km away. Similar charcoal counts at a greater depth covering an interval of about 150 years imply a frequency of 20 to 40 years for major fires--a frequency not unlike that of the modern period of attempted fire suppression.

THE RECORD OF FIRE IN THE DISTANT PAST PROVIDED BY LAKE SEDIMENTS

The tree-ring record of fire history in the pine forests of northern Minnesota leaves little doubt that fire has been a major factor in determining forest composition, and the charcoal record in short cores of lake sediment, as described above, indicates that the mosaic of forest types controlled by periodic fires has maintained a relatively uniform overall composition for many centuries, at least as far as can be detected by stratigraphic pollen analysis. And in some areas the record of regional stability is documented for several millennia, so that one can think of the mosaic as a fire climax that has persisted through many generations of trees (H. E. Wright 1974). But what of the longer term record through the 10,000-15,000 years of postglacial time, or even longer in unglaciated areas?

Pollen analysis of long cores of lake sediment show that in most areas vegetation has changed substantially in this time range. In central Minnesota, for example, the dominant vegetation changed from spruce forest to pine forest about 10,000 years ago, then to oak forest and even prairie, culminating about 7,000 years ago, followed by a reversal to the modern pine forest. These changes almost certainly are a result of a trend to warmer, drier climate, followed by a reversal. It would be possible to determine fire frequency for different vegetation types on a semiquantitative basis by stratigraphic charcoal analysis of representative segments of lake-sediment cores in this area, as Cwynar did at Greenleaf Lake for the interval 770-1270 A.D. (fig. 9). This was attempted for the transformation from spruce forest to pine forest 10,000 years ago, with the hypothesis that spruce is less well adapted to fire than pine and thus might show a lower fire frequency (Amundson and Wright 1979). The sample interval was not sufficiently small to establish an interpretable stratigraphy, however. It could be concluded only that fires occurred in both forest formations (fig. 10).

In the pine forests of the Atlantic Coastal Plain and the Appalachian Piedmont in southeastern United States, fire is an important ecological factor (Christensen this volume). Pollen diagrams from this region (fig. 11) indicate that before 5,000 years ago pine was much less common than today, and that the dominant pollen type was oak (Watts 1979). Several explanations can be offered for this transformation, ranging from climatic change to delayed migration of southern pines from earlier refugia. Whether or not fire frequency played a role in this transformation is uncertain.

In the hardwood forests of the Appalachian Mountains fire is not important, and regeneration of forest stands is abetted by windstorms instead. No studies of charcoal stratigraphy have been made in this region, however. The climate there is warm and humid enough and the microbial activity is sufficient so that detritus does not accumulate on the forest floor to an extent great enough to fuel extensive fires.

Another area with low fire frequency is southeastern Labrador, where the climate is cool and humid. Although the forest consists dominantly of black spruce, which regenerates readily after fire, the forests of all of Labrador completely lack jack pine (the fire tree par excellence), in contrast to the rest of the boreal forest farther west. Except for the lowland near Hamilton Inlet and Goose Bay, where the climate is milder and tree growth is sufficient to sustain logging operations, the black spruce forest of southeastern Labrador is depauperate, pockmarked with openings, and commonly marked by a thick mat of mosses and other ground plants that show little

KIRCHNER MARSH

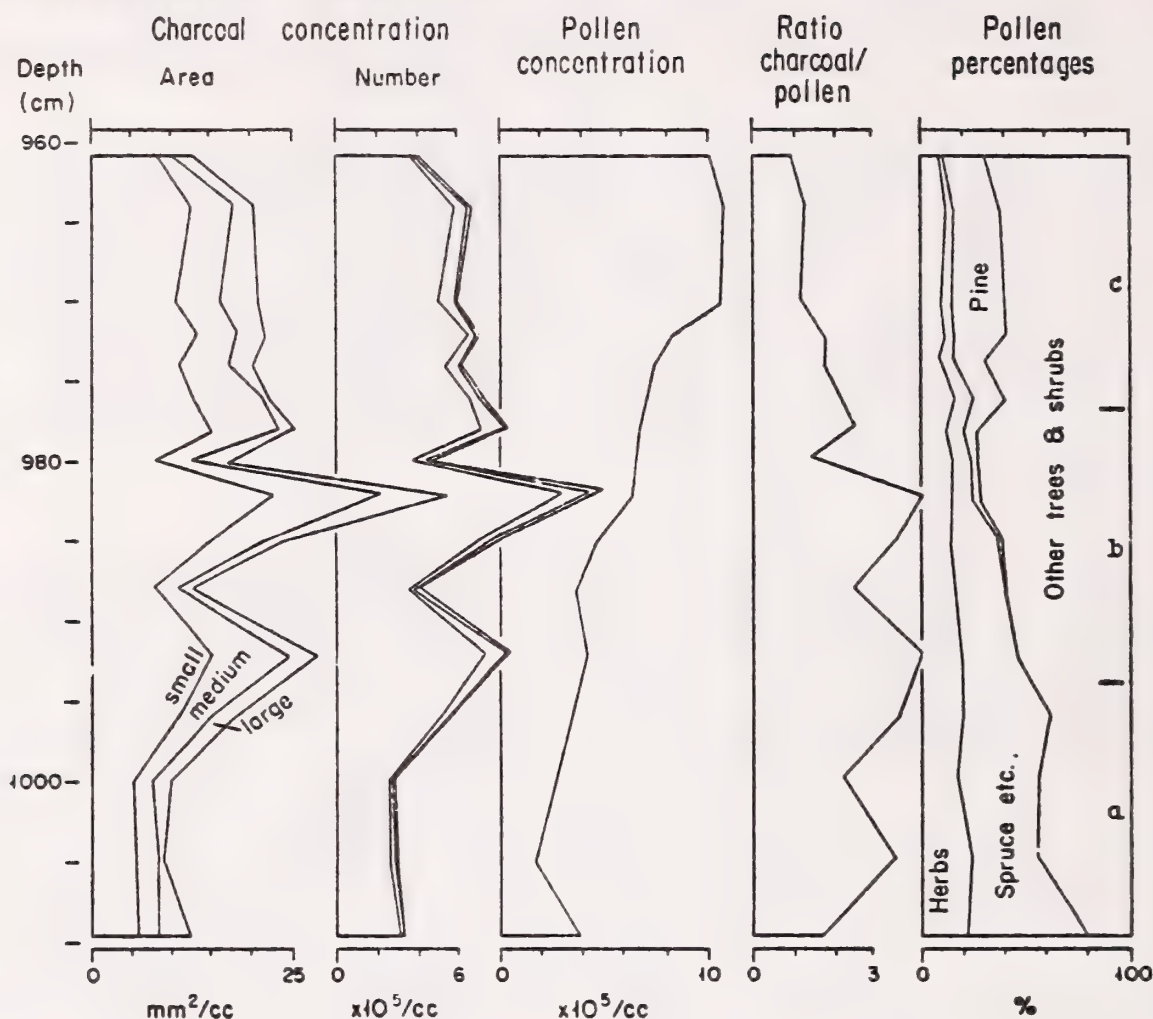


Figure 10.--Charcoal stratigraphy for an interval of 50 cm (representing about 200 years) at Kirchner Marsh, southeastern Minnesota, expressed as area and as number of small, medium, and large particles per cc of sediment. The summary pollen percentages show that the change from dominant spruce to dominant pine was not accompanied by a change in charcoal abundance. From Amundson and Wright (1979).

HACK POND, Virginia

Alan J. Craig, 1968

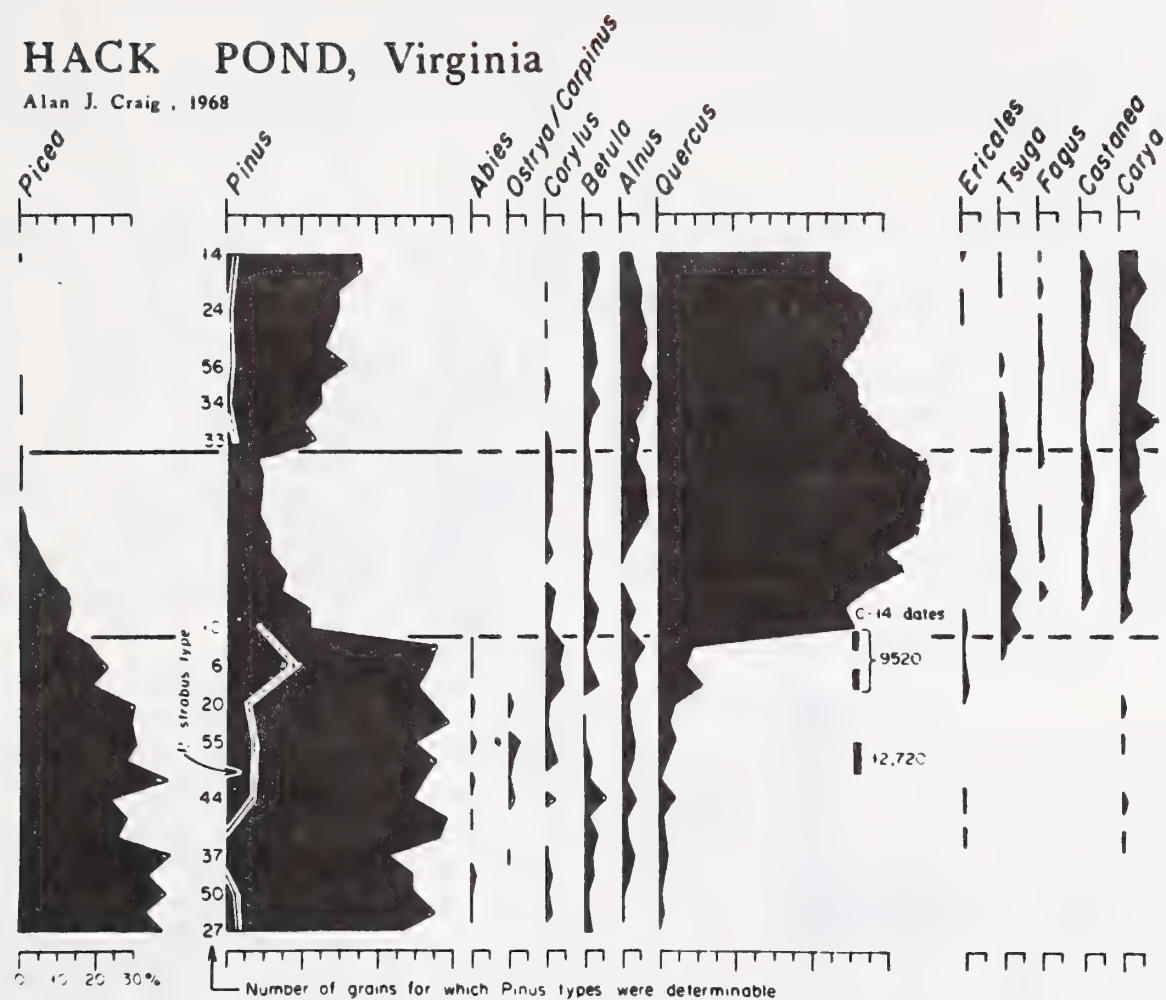


Figure 11.--Pollen diagram for Hack Pond, Shenandoah Valley, Va., showing transformation from dominant oak to dominant pine, as characteristic for much of the southeastern United States. Many species of southeastern pines are adapted to fire, but it is not known whether the vegetation change recorded here resulted from a greater frequency of fire. Redrawn from Craig (1969).

sign of recent fire. Poorly drained areas are covered with sedge marshes and string bogs, which climb up gentle slopes and invade the forest. Much of the landscape seems destined for take over by wetlands.

The lakes in southeastern Labrador are brown-water lakes, being affected by drainage of dissolved humic materials from the wetlands, and the sediment currently being deposited is "dy"--the very-fine-grained organic substance characteristic of such dystrophic lakes. The historical development of these lakes and landscapes has been worked out in a preliminary way by Lamb (1979) from stratigraphic studies of lake sediment (fig. 12).

It appears that white spruce invaded a shrub tundra of alder and dwarf birch in southeastern Labrador as early as about 9,000 years ago, soon after deglaciation, according to the pollen record and radiocarbon dating, and that an open spruce park tundra prevailed for several thousand years. The hill slopes became stabilized early in this phase as frost disturbance decreased, and normal organic sediment (gyttja) composed largely of algal detritus was deposited in the lakes. About 6,000 years ago balsam fir increased at the expense of white spruce, and a closed forest of fir, white and black spruce, and paper birch then probably developed, lasting for several hundred years. This type of forest is found today in southern Labrador on the best sites, i.e., those neither excessively wet nor dry (Wilton 1965), but not in areas close to the northern forest limit. About 5,000 years ago fir and birch decreased sharply, and spruce attained the almost sole dominance it has since exerted.

It was just at this time that the lake sediments studied changed from gyttja to dy, reflecting inflow of dissolved organics from the hill slopes. It is likely that the forest change involved a shift from mesic conifers to black spruce, as the carpet of mosses, ericaceous shrubs, and conifer needles built up on the forest floor in the more poorly drained areas and created acid conditions favorable for black spruce. Lowland bogs probably were widespread by this time, as suggested by the fact that the carbon dates from basal peats in southern Labrador are almost all in the range of 6,500 to 5,000 years ago--not older. The growth of bogs up gentle slopes may have begun at this time, aided locally near lake shores by progressive development of ice-push ridges, which impede the drainage from hill slopes. This process has led to the progressive paludification so apparent today in the landscape of southeastern Labrador. Radiocarbon dates indicate that the deposition rate of the sediment decreased in the last few thousand years, reflecting reduced lake productivity. The influx of spruce pollen also decreased, presumably the result of decreased abundance or productivity of the spruce trees as paludification proceeded.

These paleoecological relations imply that fire has been relatively unimportant in the last few thousand years in the boreal forest of southeastern Labrador, for frequent fires tend to consume the forest floor and inhibit the buildup of peat. In this situation the nutrients derived from rock weathering are not recycled within the mineral soil and biomass but are stored in the undecomposed forest floor and the growing peatlands. As the peat thickens the living plants lose contact with the nutrient supply from mineral soils, and the plants that succeed are those that can tolerate the low nutrient status. The depauperate black spruce forest, with undergrowth of mosses and ericaceous shrubs and with reproduction almost entirely by layering, is moist enough to escape severe burns, and it is this vegetation type that is the most extensive in southeastern Labrador today.

The postulated progressive paludification of the boreal forest of southeastern Labrador may reflect higher levels of precipitation and lack of summer drought there compared to central and western Canada, which have a continental climate, frequent fires, and abundance of jack pine adjusted to a fire regime. Only in the vast Hudson Bay Lowlands or in the great Red Lake peatland in northern Minnesota can similar

EAGLE LAKE, Southeastern Labrador

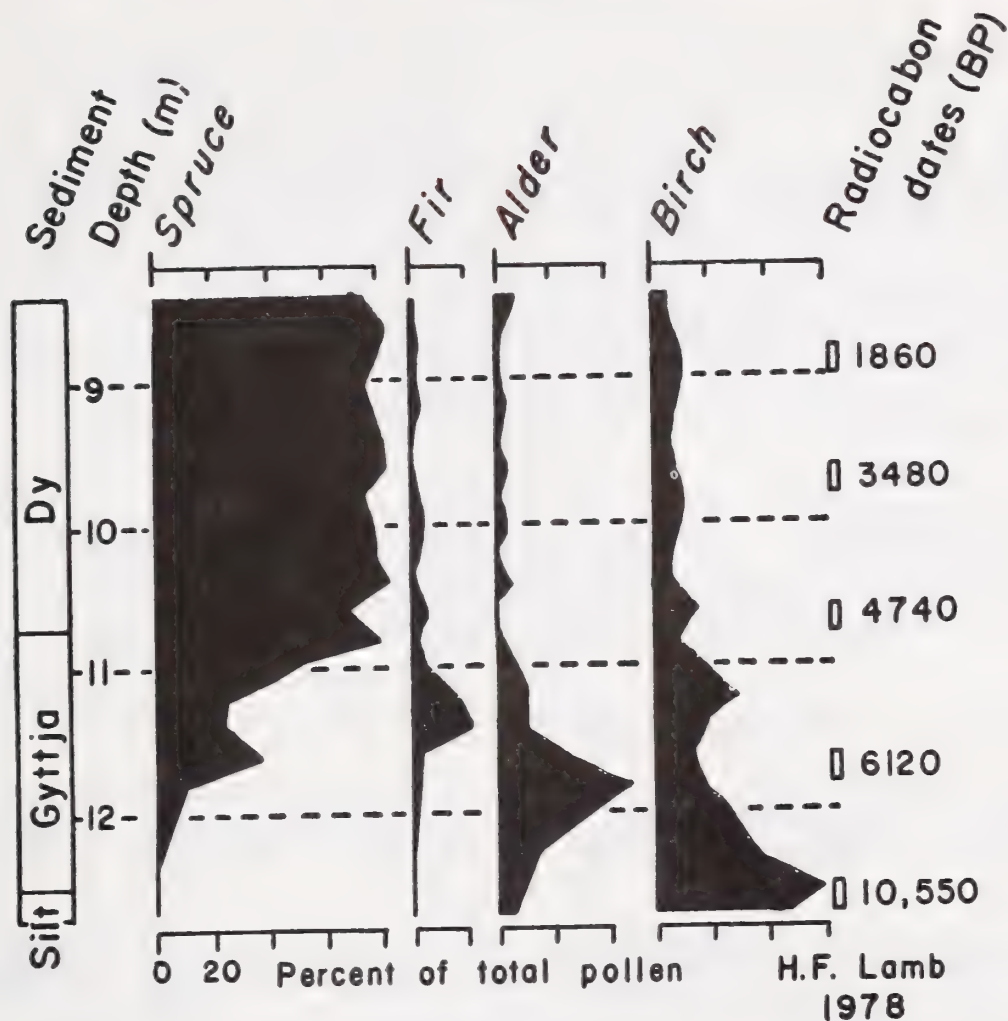


Figure 12.--Summary pollen diagram for the sediments of Eagle Lake southeastern Labrador, showing some of the evidence for the succession from shrub tundra and spruce parkland to a forest of white spruce, fir, and paper birch (about 6,000 years ago) and then to black spruce forest (about 5,000 years ago), as the lake sediment changed from predominantly algal detritus (gyttja) to a sediment charged with humic substances (dy) resulting from the development of peat in the drainage basin. Redrawn from Lamb (1979).

broad-scale paludification be demonstrated. In the latter area the poor drainage on the floor of Glacial Lake Agassiz reduces the fire frequency compared to that of the surrounding upland; the climatic change of about 4,000 years ago facilitated the western expansion of conifer forest and the accumulation of peat.

CONCLUSIONS

This review of some of the interactions of fire and water started with comments on the low potential of forest fire to produce flooding and eutrophication of streams and lakes, considered the role of streams and lakes in controlling the spread of fires at the prairie/forest border, and terminated with accounts of the sedimentary record of past fires and with speculations on the importance of fire in holding down the paludification of humid northern landscapes, a gradual process whose history is revealed by the stratigraphic study of lake sediments. Many other interactions could be discussed, for an aquatic ecosystem relies heavily on the terrestrial ecosystem in its drainage basin to supply water, nutrients, and sedimentary particles. Not the least important is the role that lakes play in preserving the sedimentary record of past events, so that our speculations on the long-range role of fire in the development and stability of forest ecosystems can be tested by careful analysis of this record. Forests do change over time for a variety of reasons, and fire may play a direct or indirect role in forest history. The elucidation of this role in the past is a challenge for the paleoecologist, working from fragmentary data, but in the absence of any such historical test the speculations of the neoecologist must remain quite hypothetical.

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FOREST INSECTS, FOREST FIRES, AND RESILIENCE

C. S. Holling

Professor

Department of Zoology and Institute of Animal Resource Ecology
University of British Columbia

ABSTRACT

Forest fire systems are compared to the balsam/spruce budworm system. Management of both has been successful in the short term in reducing the probability of fire or preventing sudden and extensive mortality of balsam. But both have resulted in conditions highly vulnerable to outbreaks of fires or budworm more costly and extensive than any before. The underlying causes are similar and are identified by analyzing (1) the equilibrium structure of the unmanaged systems, (2) the effects of management on this structure, and (3) the adaptive responses of management institutions to this surprise.

KEYWORDS: stability, spruce budworm, resource management, adaptive.

INTRODUCTION

I have one main objective for this paper. That is, to take the resilience concept (Holling 1973) just one step further. Ecology, in common with many sciences, tends to emphasize isolated parts of the whole. There are penetrating theoretical and mathematical studies that pay, at best, passing gestures to empirical studies and application. There are empirical studies of "natural" systems that emphasize the need for rigorous analysis of reality and stand in splendid isolation from both theory and application. And there are studies of applied ecological management that draw neither on a rigorous empirical understanding nor on testable concepts from ecology or the policy sciences.

In attempting to achieve my objective, I will focus on two specific systems and analyze these by integrating theories of stability with empirical studies of the unmanaged, "natural" systems and of the response of those systems under different kinds of management. The core of the paper will compare two ecological systems that have probably been more intensively examined and understood than any others: spruce budworm/forest interactions and fire/forest interactions. After reviewing the natural dynamics and management consequences of each, I shall review the advances that have

been made since the resilience concept was first explored. From this, further advances in understanding of the concept emerge. Finally, the need for the analysis of institutional behavior as well as ecological behavior is highlighted.

Success and failure are partners. Forest fire detection and suppression policies have historically been dramatically successful in reducing the frequency and extent of fires. But as a consequence of that success, fuel has accumulated in protected areas, raising the threat of more damaging and extensive fires than those that occurred naturally. Natural fires in the mixed conifer forests of the Sierra Nevada, for example, occurred frequently enough to produce burns of low intensity (Kilgore 1973) that limited the accumulation of fuel. Tree mortality was minor; and fire, by preparing a seedbed, cycling nutrients, and establishing a mosaic of age and vegetation types, was responsible for maintaining the persistence of giant sequoia and various pine species. But fire control practices excluded fires over extensive areas, producing conditions suitable for highly intense fires and attendant high tree mortality over extensive areas. Hence the very success of fire control policies threatened the persistence of the system they were designed to protect. From that viewpoint the success was a failure.

But that is a narrow interpretation. As that surprise began to be perceived, it was documented and the causal links were analyzed and demonstrated for a variety of forest ecosystems (reviewed in Kilgore 1976, Heinselman 1971, Sanderson 1976). A pattern of understanding emerged with consequences to management of specific areas; an understanding that had generality as well. As a result, the U.S. National Park Service fire management has changed some of its policies, restoring fire to its natural role by applying prescribed burning and letting certain lightning fires burn unhindered.

From a broader perspective, then, this history is one of success. Against considerable institutional commitment to fire suppression policies, an adaptive change occurred in response to a surprise. The point is that we can learn from failure. Successful policies are those which, in probing the unknown, yield signals of surprise and failure soon enough that adaptation can occur.

The ingredients of the familiar fire control history are not restricted to fire. The same features are found in a large number of renewable resource problems. Effective reduction in the probability of flooding can lead to established use of flood plains which leaves them subject to enormous costs if floods do occur (Burton and others 1977). Effective protection and enhancement of salmon spawning can lead to more predictable success that in turn can increase fishing and investment pressure. Less productive stocks become extinct, leaving the fishing industry precariously dependent on a few stocks (Larkin 1979). Successful suppression of spruce budworm populations in eastern Canada certainly preserved the pulp and paper industry and employment in the short term by partially protecting the forest, but left the forest susceptible to an outbreak covering an area, and of an intensity, never experienced before (Clark and others 1979).

In each of these cases the policy successfully reduced the probability of an event that was perceived as being socially or economically undesirable. Each was successful in its immediate, short-term objective. Each resulted in the system evolving into one with qualitatively different properties. Fire suppression led to unnatural accumulations of fuel and changes in forest structure. Flood control led to more intense and inflexible land-use patterns and entangled legal and institutional structures. Salmon protection and enhancement led to more intense fishing and changed stock composition. Spraying of budworm led to greatly lowered or delayed tree mortality and moderate levels of infestation in vulnerable stands over larger areas. And all led to institutions whose goal was to implement the policy - to fight fires, build dams, hatch salmon, and spray insects.

But not all of these institutions have responded to surprise with adaptive responses, as has the U.S. National Park Service. In some cases, institutions continue to implement original policies in the face of their failure, with easy retreat and adaptation becoming more and more difficult.

The key question, then, is not how to design to predict and reduce surprise, which is a necessary but never attainable goal, but how to design and manage surprise adaptively. As a step in that direction, I will compare the forest fire management system, where adaptation to surprise has occurred, to the budworm management system, where it has not occurred.

Three topics will be considered. The first concerns the features of the causal structure that account for the surprise. The second incorporates causal structure and variability into a further conceptual development of our understanding of how systems respond to disturbance. And the third speculates on the features that permit adaptive responses to surprise.

ANATOMY OF SURPRISE - TWO CASES

It is a truism to say that unexpected and costly surprises or crises of management occur because of inadequate understanding of the system being managed. But when crises of a similar type are recurrent features of a large number of different systems, then it suggests a causal structure, at some level, that has considerable generality. This section develops one step in identifying that common structure by comparing the budworm- and fire-dominated ecosystems.

The Spruce Budworm/Forest System

The spruce budworm is the most widely spread destructive forest insect in North America. It ranges from Virginia to Labrador and west across Canada into the Northwest Territories. In the northeastern part of its range the budworm periodically undergoes severe and extensive outbreaks, imposing heavy defoliation and high mortality on balsam fir and white spruce. Analysis of tree rings of surviving trees (Blais 1965, 1968) indicates a distinctive 30- to 45-year period between outbreaks in New Brunswick since the early 1700's. During outbreaks the numbers of budworm can increase by three orders of magnitude over a 3- to 4-year period. Once the outbreak is initiated in a sufficiently large area, it spreads over thousands of square kilometers, finally collapsing after 7 to 16 years. The outbreaks cause major destruction of balsam fir in mature forests, leaving less susceptible spruce and nonsusceptible white birch, and causing a dense regeneration of fir and spruce. Between outbreaks the insect is exceedingly rare; the young balsam grow, together with spruce and birch, to form dense stands in which spruce and birch, in particular, begin to suffer from competition. This process evolves to produce stands of mature trees with balsam a predominant species. The stage is then set for another outbreak.

Superficially, at least, there is a similarity between the budworm system and the Sierra Nevada fire system mentioned earlier. Each has a distinct period between "outbreaks"; each dramatically depletes its "food"; each can spread from local regions to engulf larger regions; and each has experienced management activities that produce conditions particularly vulnerable to more intensive or extensive outbreaks. And just as it is now broadly appreciated that fire is an integral part of many ecosystems, determining species, age, and physical composition (Heinselman 1971, Kilgore 1973, Vogl 1974), so budworm is a prime determinant of the structure of the balsam fir/spruce forests. The interplay between frequency and intensity of budworm outbreaks and the competition among different tree species and climate lead to a persistent association of the fir-spruce-birch complex (Baskerville 1975). Change the word "budworm" to "fire" and change the names of the tree species, and the argument becomes identical to that expressed for a number of fire-dominated forest ecosystems.

But that similarity might be superficial, or similar only in terms of effect, not cause. If the two systems had a similar causal structure as well, the aim of understanding the general sources of surprise would be better met. I shall first consider the budworm system, in part to explain its causation and in part to provide a language and framework within which to consider forest fire systems.

The budworm system has been the subject of intensive research and management efforts since the late 1940's (Morris 1963, Belyea and others 1975, Prebble 1975). That extensive body of data and understanding recently led to the development of a policy analysis in which one element was the development of a simulation model that would capture the dynamics of the budworm system (Holling and others 1976, Jones 1977, Clark and others 1979). The model was designed explicitly to be part of a set of analyses that would generate a range of alternative strategies for regional management, as distinct from local or stand management. This design required models and analyses of the biological interactions of harvesting and insecticide control activities of man, and of alternative objectives so that past management could be evaluated and alternatives generated.

The biological part of the model concentrated on the minimum number of variables necessary to capture the different modes of behavior of this system in different regions under different kinds of management. Four sets of variables proved to be essential: budworm and its associated mortality, reproductive and dispersal processes, foliage condition, and host trees by age and weather. The 7 million hectares of New Brunswick were divided into a mosaic of 393 patches governed by local interactions; these patches were linked by insect dispersal. The model adequately predicts observed patterns in space and time for different regions of North America under natural and historical management conditions.

But to do that and also be responsive to development of new management strategies, the model is too complex for easy comprehension. Local interactions in each patch require functions linking 78 variables, leading, hence, to over 30,000 variables for the full region (78×393). Using topological approaches, however, Jones (1977) and Ludwig and others (1978) were able to compress the causation into a simpler and hence more comprehensible form. The simulation model captures detailed explanation; the topological representations capture simple understanding.

The 78 variables expressing the local interactions can be collapsed into three sets: budworm, foliage condition, and volume of crown per hectare. Each of these variables operates on a different time scale. Budworm operates on a scale of months; foliage replacement occurs in the order of 7 to 10 years; and volume of crown is related to the age of trees whose generation time is measured in decades. That sequence from fast (budworm) to slow (tree) variables is the first step in the analysis.

The second step is to determine how the fast variable (budworm) would behave if, for the moment, the slow variables (foliage and tree crown volume) were held constant. That behavior can be deduced by measuring the rate of budworm population growth at different densities of budworm. This is shown in figure 1 where the rate is expressed as the ratio of the density in generation $t + 1$ to the density in generation t . The three sample curves shown represent three levels of forest maturity.

Such growth-rate curves condense the reproduction and survival functions contained within the simulation model. For example, the decline of the curve at high densities is largely the consequence of competition for a limited supply of foliage; the dip in the curve at low densities reflects predation of large larvae by vertebrate predators, augmented by parasitism.

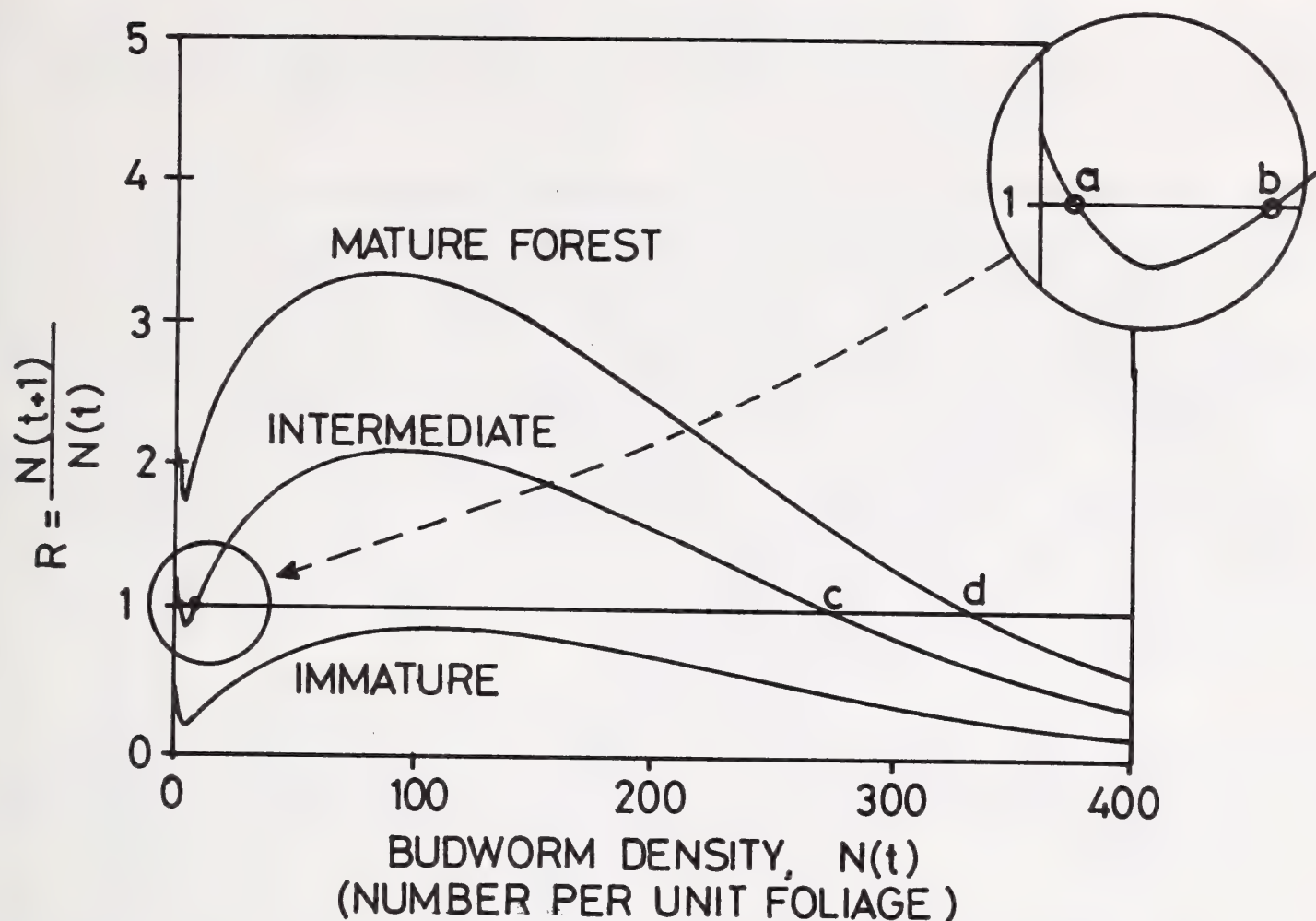


Figure 1.--Growth-rate curves for budworm populations for three different forest conditions. a, c, and d are locally stable equilibria; b is an unstable equilibrium.

Behavior of populations depends on the location and properties of the equilibria which occur wherever the growth rate, R , equals one. Consider the intermediate curve in figure 1, for example. Three equilibria occur - at a, b, and c. With the slow variables held constant, a represents a stable equilibrium, for if densities are a little less than a, populations will increase in the next generation and if densities are a little larger, populations will decrease. The same is true of point c. Point b, on the other hand, is an unstable equilibrium. If densities are a little below b they will decrease towards a; if above b populations will increase to c.

The third step is to relax the requirement that the slow variables be held constant. When the forest is immature (the lower curve in fig. 1), growth rate is less than one for all densities and populations are in a decrease phase. No outbreak is possible. But now we can imagine the forest growing and crown volume increasing towards the intermediate curve of figure 1. The three equilibria - a, b, and c - appear. Low budworm densities will increase and perhaps achieve a. An outbreak is only possible if, somehow, densities can increase above b. This can happen if there is a significant indispersal of moths from some other area into the local patch. At this point we begin, therefore, to see the role of spatial heterogeneity. It can also occur if weather conditions improve enough to raise the curve sufficiently that the lower dip rises above $R = 1$. Under these conditions populations increase towards the outbreak levels represented by c. Although that equilibrium is stable for budworm, it is not stable for the slow variables, i.e., foliage and trees. The defoliation is so intense that trees die over a 3- to 5-year period, cycling the populations to low numbers and the forest to a less mature state.

If, however, neither indispersal nor weather triggers an outbreak in intermediate aged forests, increasing tree growth results in a mature forest where the equilibria a and b disappear. Barring weather conditions unfavorable to budworm, an even more severe outbreak is inevitable.

Since this interpretation depends only on knowing the position and stability properties of equilibria, a more succinct summary can be obtained by plotting all the equilibrium densities of budworm as a function of the slow variable, tree crown volume (fig. 2). This produces an "equilibrium manifold," which separates regions of increase from regions of decrease. The equilibrium manifold is hence the zero isocline where the rate of increase of the population is zero. The upper surface represents the upper equilibria of figure 1 (c and d), the line near AB represents the lower equilibria (a), and the underside of the manifold represents the unstable equilibria (b). The trajectory in figure 2 shows a typical unmanaged outbreak pattern. Segment AB is the long endemic period beginning with an immature forest. As the forest grows, budworm populations remain low until the lower equilibrium disappears at B. Segment BC is the initiation of the outbreak phase with populations rising rapidly to the upper equilibrium. Trees suffer extreme mortality at these densities and the outbreak collapses along CA to restore the cycle.

When the other slow variable, foliage, is added to the representation, the equilibrium manifold becomes a surface (fig. 3). Again the arrows indicate a typical outbreak sequence. While this figure does help give an understanding of underlying causes of the dynamic behavior of this system, it only represents the equilibrium manifold for budworm.

In the fourth and final step, therefore, the manifolds for the other variables - trees and foliage - are generated in a similar manner. It is the interrelation between these surfaces that determines the pattern over time. Figure 4, for example, shows the manifold for tree crown volume laid over the budworm manifold of figure 3. The places where these two manifolds intersect (line AB) represent the only places where it might be possible to have a stable equilibrium for both budworm and trees. But that condition could only be a reality if the stable portion of the manifold for foliage, the final variable, also intersected the line AB. That manifold is folded somewhat like the budworm manifold, with one surface representing the set of equilibria that is stable for foliage and a reflexively folded surface that represents the unstable equilibria. For values of foliage below this unstable surface, foliage production cannot match foliage depletion and the foliage variable moves to extinction. Although it is difficult to show in a figure like figure 4, it happens that this manifold lies under the major portion of the budworm manifold and there is no intersection with line AB. (A more detailed treatment of these manifolds and their interrelation can be found in Ludwig and others 1978.)

Hence this unmanaged system, as represented by this model, is in a state of continual disequilibrium. If one variable is on its equilibrium manifold, the others are usually not on theirs. If two variables, like the budworm and trees, happen to be simultaneously on their respective equilibrium manifolds, the remaining variable is never on its equilibrium manifold. This is a system under continual dynamic change, quite independent of any exogenous stochastic disturbances. Analyses of conditions near equilibria that are stable for all variables, like those presented by Webster and others (1975), are simply irrelevant. There are no equilibria. Moreover, concepts of stability that emphasize an ultimate condition where all variables achieve specific values that remain more or less constant over time have limited utility.

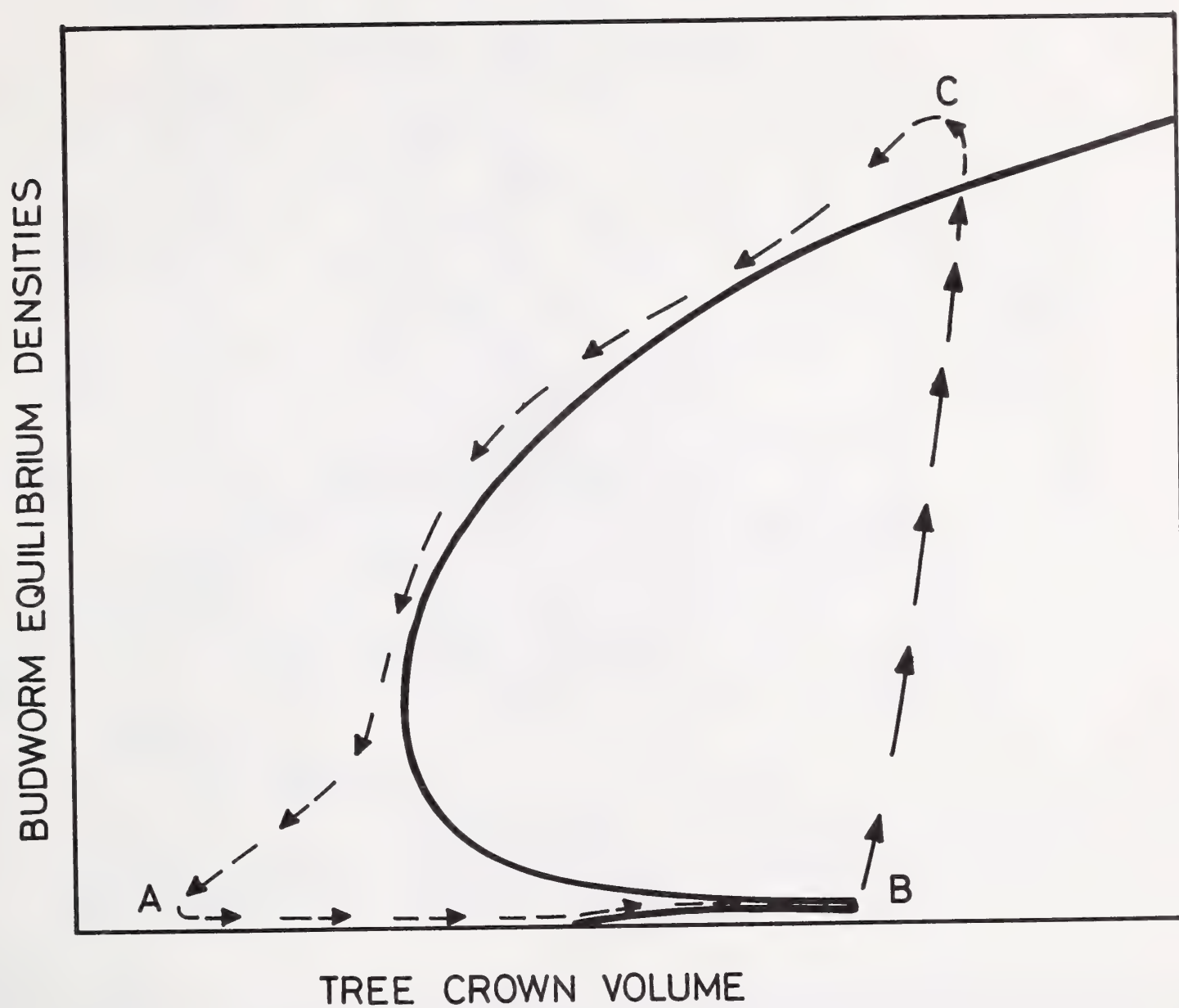


Figure 2.--Equilibrium densities of budworm as a function of the crown volume. The arrows show a typical trajectory for an unmanaged outbreak, starting with scarce budworm and an immature forest (A), to a mature forest and the release of budworm (B), to a budworm outbreak (C) followed by tree mortality.

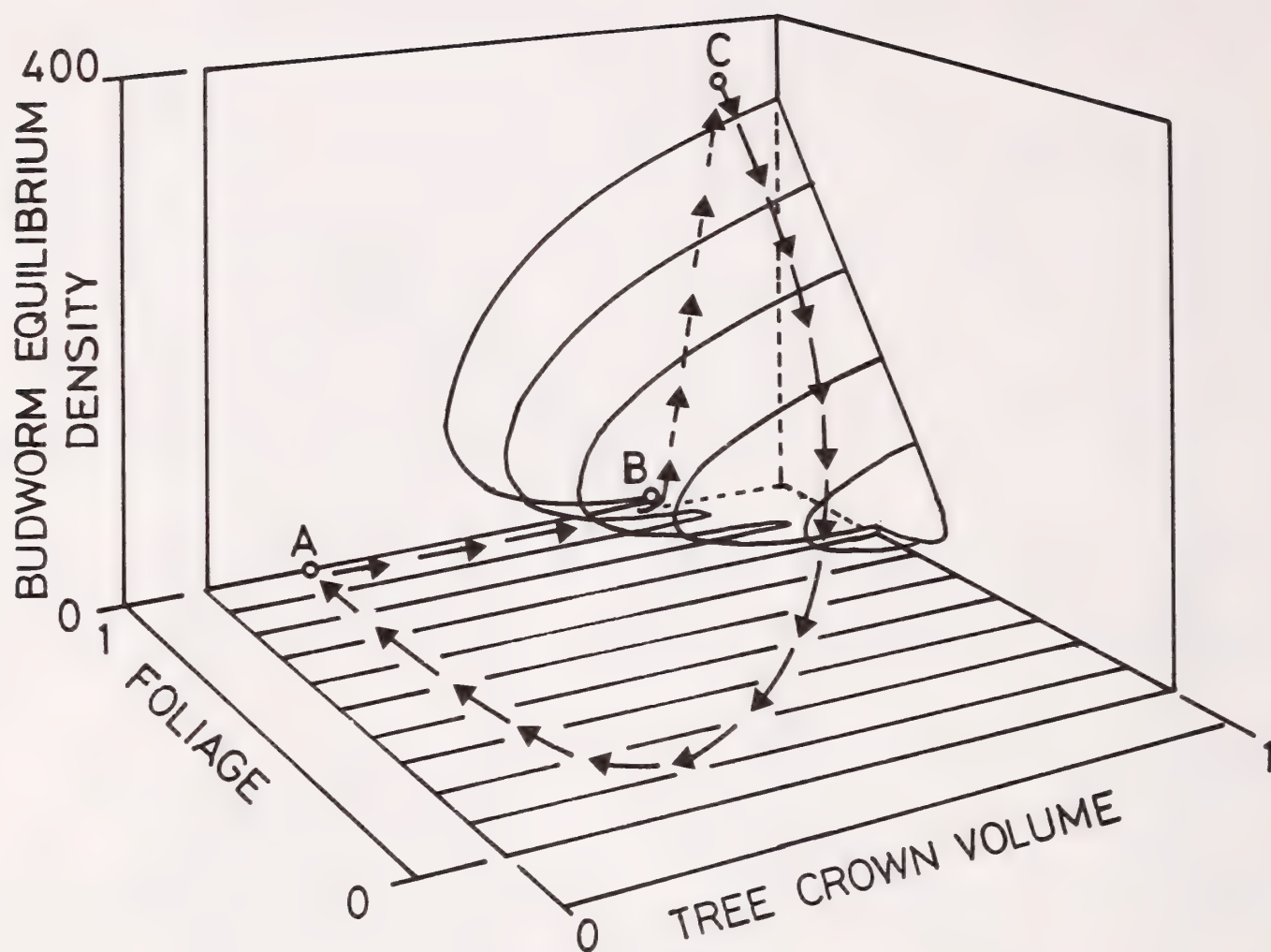


Figure 3.--Equilibrium manifold for budworm as a function of foliage and crown volume. The trajectory shows a typical unmanaged outbreak sequence.

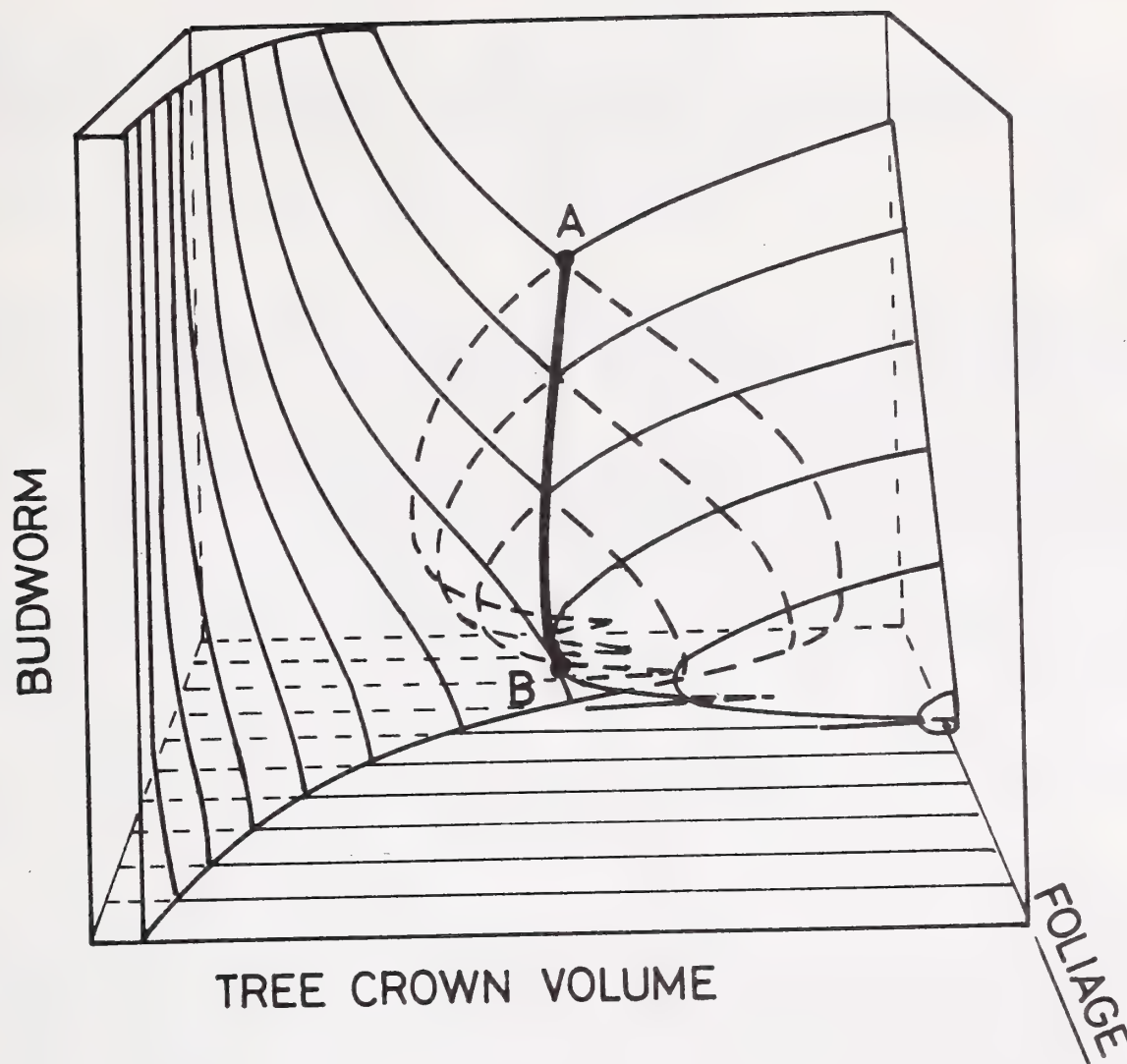


Figure 4.--Overlay of the equilibrium manifold for tree crown volume against the budworm equilibrium manifold of figure 4. The line AB is where the two manifolds intersect.

Despite this picture of ever-changing variables tracking ever-changing equilibrium surfaces, the system is still a resilient one. It still persists in the face of major disturbances - both natural and manmade. Moreover, that variability, generated as an inherent part of the internal dynamics of disequilibrium, maintains the mixture of species and degree of spatial heterogeneity (or better, homogeneity) of the fir-spruce-birch forests of east-central North America. I will return to that view of resilience later.

The search for sources of surprise in the budworm system would be incomplete without a discussion of management strategies and their interaction with the biological dynamics described thus far. In New Brunswick, management has largely relied on an insecticide spraying program since the early 1950's. The intent was not to attempt to eliminate the pest, but to protect the forest. Hence stands were sprayed whenever trees were stressed by heavy defoliation, particularly over more than 1 year. That succeeded in the short term in preventing a massive outbreak with rapid and extensive tree mortality. But after 20 years of spraying, a number of unexpected surprises began to be perceived. First, budworm populations persisted at moderate levels and spread over larger and larger areas. Second, while tree mortality was delayed, it was not eliminated. The level of stress, although lower, slowed tree growth, caused top mortality, and increasingly caused the death of whole trees. Third, insecticide costs have escalated, as has public opposition to spraying, in part because of a potential

health hazard from the insecticide carrier (Crocker and others 1976). And yet there is no easy retreat. Cessation of spraying would result in an outbreak covering an area larger than any affected before, just when the forest industry and economy have become even more dependent on the balsam forest as a consequence of the earlier, perceived success.

The underlying sources for the surprises lie partly in the features of ecological behavior, described above, and partly in the features of institutional behavior. I shall touch on institutional behavior when the lessons from fire management and budworm management are compared. For the moment, consider again figure 4, which summarizes the ecological causation for an unmanaged system. The historical rules or strategy for applying insecticide can be roughly described as aimed at killing 80 percent of the population whenever the foliage condition deteriorated to a fixed value and budworm was fairly abundant. If figure 4 were reconstructed with this additional mortality, then the budworm manifold would suddenly change below some intermediate foliage value and intermediate budworm densities. Essentially the upper surface of the manifold would be lower. Under these conditions, the manifolds for the three variables--budworm, foliage, and trees--intersect at one point. Hence, the system is no longer one of dynamic disequilibrium where there is no equilibrium for all three variables simultaneously. Now an equilibrium exists and around that point, stable for all variables, is a region (or stability domain) in which trajectories move to that equilibrium. When these rules are incorporated in the simulation model, where all the time dynamics are explicitly represented, tree crown volume declines slowly to an equilibrium, because stress has been relaxed enough to allow a balance between crown mortality and growth. Budworm and foliage then cycle with a periodicity of about 8 years. In the managed system the periodicity is set by the generation time of foliage. It is a world with a forest maintained in an eroded condition with moderate and fluctuating densities of budworm that spread over larger and larger areas. If spraying stops, the original dynamics hold and a much more extensive outbreak with high tree mortality occurs.

The ecological sources of surprise in historical or other management strategies thus lie in the topology of the system - in the form and relationships of the manifolds. The key features can be summarized as follows:

1. The key variables have distinctly different speeds - fast for budworm, slower for foliage, and slowest for trees.
2. With other variables held constant there are three stable equilibria for budworm (zero, low values above zero, and high values), two stable equilibria for foliage, and one for trees.
3. The movement of budworm populations from the lower to higher equilibria can be triggered in a variety of ways, e.g., maturation of the forest, invasion of moths, or weather favorable for budworm survival. Hence local, spatial, and stochastic processes can all contribute to outbreaks. There is not a single cause of outbreaks.
4. The equilibrium manifolds for all three variables in the unmanaged system do not intersect at one point. That, and the differences in the speed of variables, generate a system in dynamic disequilibrium with high variability, one in which the periodicity is set by the slowest variable, trees.
5. Management rules change manifolds. In the historical management example the change in the budworm manifold causes all three manifolds to intersect, producing persistent semioutbreak conditions and reduced variability. Periodicity is set by the foliage.

6. Other surprises of management can be deduced from the manifold. For example, the lower equilibrium for budworm is in part caused by bird predation. If management directly or indirectly affects bird populations or their feeding habits, then those strategies dependent on that lower equilibrium will face future surprise.

Fire and Forests

The above analysis of the budworm/forest system provides a framework to interpret the causes and effects of fire in forest systems. The aim of this section is to use that framework to identify the similarities and differences in the two systems, as a step in an effort to generalize.

Simulation models have been developed to predict fire behavior and its effects in forests, with a purpose similar to the budworm/forest study (Clark and others 1979), i.e., as an aid to explain, manage, predict, and communicate alternatives (Rothermel 1972, Kessell 1976). But such models, and the systems they represent, have not been analyzed with the topological approaches described above. To repeat, simulation models can be admirable devices to capture explanation; topological and qualitative methods are useful to encapsulate understanding.

But we can imagine the form such a topological representation might take if we follow the steps described for the budworm/forest system. Consider the mixed conifer forests of the Sierra Nevada, for example (Kilgore 1973).

First, a minimum set of variables could potentially include fire intensity; fuel quantity, quality, and density; and kinds and condition of vegetation. As in the budworm/forest system, each operates on a distinctive time scale--fastest for fire intensity, slower for fuel, and slowest for trees. Each set could be divided into a large number of variables, but for the moment it is better to start with as simple a representation as possible, adding detail as it becomes necessary. Since extensive mortality of trees from fire was rare in the natural system in the Sierra Nevadas, it is useful, initially, to imagine the tree species and age distribution over extended areas in a stable, persistent equilibrium. We then explore how the remaining variables might interact when the tree variables are kept fixed at their equilibrium.

The resulting skeletal model would include fire intensity and fuel. Fire intensity is conveniently measured as rate of energy release per unit length of fire front (Byram 1959). Hence the model will not focus on a fixed spatial area but on the moving fire front itself, with the fire continually renewed with fuel as it is consumed. The fuel variables are more complex since quantity, moisture content, physical and chemical structure, and spatial distribution are all important. In this first simplified topological representation, however, an aggregate measure of fuel condition can be visualized for purposes of illustration.

The second step is to determine how fire intensity (the fast variable) would behave if fuel condition was imagined as being constant at different levels. The resulting equilibrium manifold could take the form shown in figure 5. If fuel condition is below A there is no possibility for a self-sustaining fire. A local ignition event would not spread and would be extinguished. Above A, however, three equilibria appear. If an ignition event generates an intensity below the bottom surface of the manifold (the set of unstable equilibria), it will self-extinguish. If the intensity exceeds that surface, the intensity will increase, attracted to the upper equilibrium surface. A sustained, spreading fire will result. As fuel condition increases above A, the intensity required to produce a self-sustained fire becomes progressively less. If we imagine that ignition events are random and frequent occurrences, with an average intensity indicated by line B in the figure, then a self-sustained fire would tend to occur whenever fuel conditions reached the value C. This simply represents Mutch's

observation (1970) that plant communities may be ignited accidentally or randomly, but the character of burning is not random. This structure can turn a random event of high frequency into a highly periodic and predictable one. That certainly seems to be the case in the unmanaged Sierra Nevada forests, where fires occurred in most areas every 7 to 9 years (Kilgore 1973).

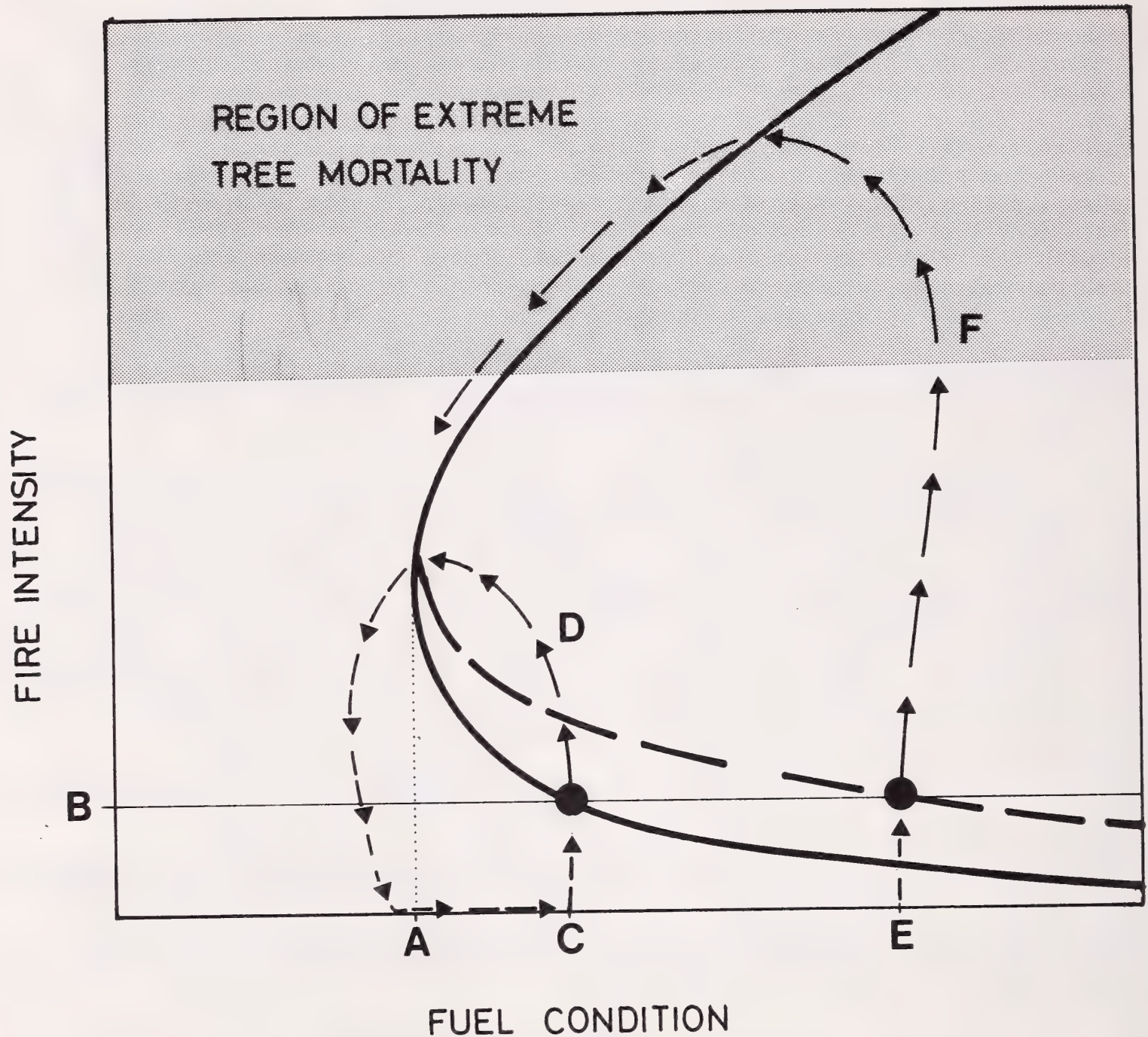


Figure 5.--Equilibrium manifold in a skeletal model of fire (see text for explanation).

In the third step we relax the requirement that fuel, the slow variable, be held constant. After a fire, fuel condition changes year by year. In the natural conditions of the Sierra Nevadas such fires were confined to the ground and it is likely that fuel accumulated progressively year by year. But fire both destroys and produces fuel, particularly if there is heavy tree mortality. Hence in some forests (e.g., lodgepole pine, Muraro 1971), characterized by major fires once each rotation, fuel condition can be high immediately after a fire, declining through decomposition, and then increasing again as the stands become mature and overmature. That sequence delays the period between fires, stretching it to be more coincident with the generation time of the trees. It takes longer to reach the value C.

But in the simpler examples where fuel increases progressively, we can imagine a trajectory (D, in fig. 5) that would be typical for the hypothetical mixed-conifer forests of the Sierra Nevadas before fire detection and suppression policies were applied. Those policies, like the budworm spraying rules, can be viewed as changing the form of the manifold. In this case the lower surface of the manifold is raised, as suggested by the dashed line shown in the figure. As a consequence, the standard fire ignition event of intensity B no longer can trigger a sustained fire at C. Fuel accumulates, as time passes, until eventually conditions make a conflagration more and more likely, despite the fire control practices. Now the sustained fire occurs at E, producing the trajectory F. Since the upper surface of the manifold is higher, a very intense fire results. In the reality of those particular forests, the trees would experience extensive mortality with unknown consequences for regeneration.

In the more natural trajectory, where fires are more frequent and less intense, regeneration restarts the cycle because such fires prepare appropriate seedbeds, cycle nutrients, and establish a mosaic of vegetation that encourages regeneration and growth (Kilgore 1973). With the more intense, less frequent fires that are a consequence of fire control, those regenerative processes will take a different route, leading to a forest of radically different composition and structure.

Because of that, the earlier skeletal model is too limited since it considered only fire and fuel. Tree variables cannot be presumed to be at a sustained equilibrium. Like the unmanaged budworm/forest system, variables change dynamically. There would thus be a minimum of three sets of variables, relating to fire, fuel, and trees. But even without continuing to the fourth step, where all equilibria conditions are examined, the topologies of the budworm and fire systems are clearly similar. Both have variables of distinctly different speeds; both have several equilibria surfaces; in both, the management practices can change the form of the manifolds; and both indicate the possibility of high variability as a result of a dynamic disequilibrium. But there are differences in behavior, in part related to different timings of variables, in part to different coupling between the variables, in part to a different frequency and impact of external stochastic events. Hence the "boom-and-bust" trajectory (F, fig 5), where there is extensive tree mortality, is the natural behavior of the unmanaged budworm system. That is not true of the unmanaged Sierra Nevada forest because of the pattern of fuel accumulation, the high frequency of ignition events, and the high combustibility of the fuel. However, there are fire/forest systems that naturally conform to the "boom-and-bust" pattern. An example is the conifer forests of central North America (Rowe and Scotter 1973, Ahlgren 1974). They behave much in the manner and for the same reasons as described earlier for fire-dominated lodgepole pine forests. Fires typically occur once in the rotation period, causing extensive mortality. In these situations the trees are adapted to allow for effective reproduction after the fire. A notable example is the development of serotinous cones of jack pine which only release seeds when subject to intense heat.

Those are differences in detailed dynamics. The key point is that the topological representations of the two systems are similar and that they provide a framework to interpret, explain, and predict different modes of behavior of different ecosystems under different management strategies. The surprises emerge in part from that topology.

RESILIENCE REVISITED

To this point the analysis of the fire/forest system basically reconfirms the analysis of the budworm/forest system. There is one additional feature of considerable importance to the resilience concept, however, that can be demonstrated for fire systems and only implied for the budworm system. Natural fires in the Sierra Nevada forests not only prevent excessive accumulations of fuel, they also maintain openings in the crown canopy. Periodic light fires kill young white firs while they are still part of the understory. Since fires have been suppressed, however, these trees have

grown to become part of the crown canopy which is thus becoming more continuous. In addition, fires burn in a highly variable pattern, producing a rich mosaic of discontinuous vegetation types and ages. Again fire suppression leads to more spatial uniformity (Rowe and Scotter 1973). Finally, as dead and living fuel accumulates, a condition is reached where vertical continuity in fuel is established between the ground and the crown. Hence when a fire occurs, not only is there more fuel, but the fire can move from ground to canopy. Once there, the fire does not encounter the normal breaks in the canopy and can spread rapidly over large areas. Such fires are qualitatively different from ground fires. Rowe and Scotter (1973) note there is at least an order of magnitude difference between the intensity of ground and crown fires.

Hence the early topological picture of figure 5 is oversimplified. There it was assumed that the spatial structure of the forest remained fixed--a parameter of a model. Now we can see that because of successful fire suppression, that parameter begins to change, to evolve, until vertical and horizontal continuity of fuel is established. Another dimension is added, as suggested in figure 6. Under natural conditions the spatial mosaic has low values for continuity of fuel from ground to crown and through the crown. Hence the "natural" trajectory (D) is driven by a small manifold. If fires are suppressed, the physical structure of the forest becomes more homogeneous until significant vertical and horizontal continuity in fuel occurs. There would then be a rather abrupt shift to the larger manifold shown, which would result in much more intense fires over larger areas.

All perceptions and decisions are based on some model of the system--intuitive, verbal, graphical, or mathematical. Some of the quantities are considered as variables. Others are explicitly or implicitly considered as parameters for convenience or because they change so slowly. It is unlikely, for example, that any management model of fire management need consider long term geomorphological changes. And yet we know such changes occur and have profound consequences for ecosystem structure. But the time scale is extremely long and it is hard to imagine how fire management activities would affect them. But other parameters are directly or indirectly affected by management. The ones directly affected have already been mentioned. They produce immediate changes in the manifold and one kind of surprise. But other parameters, like spatial homogeneity, are indirectly affected by management and produce delayed surprise. They initially appear to be fixed because they are the result of a dynamic balance achieved by the historical variability of the system. Change the variability through management, the balance shifts, and the presumably fixed parameter starts to change. Reducing the incidence of fires and reducing variability in budworm densities will result in parameter evolution, in changes in the basic structure of the system as the result of shifts in behavioral, physiological, ecological, or evolutionary balances. Moreover, as in the example of fuel continuity, the shifts might be abrupt.

Many ecosystem parameters potentially can evolve to produce fundamental changes in ecosystem structure. Grassland systems in humid climates, for example, are typically maintained by frequent intense fires which prevent tree regeneration and growth (Vogl 1974). We can imagine two prime variables--standing biomass as a measure of gross ecosystem properties, and fire frequency or intensity as a representation of the results of stochastic events and of the fuel/fire processes described earlier. In this case, fire would be a fast variable and standing biomass would become a slow one. There is insufficient evidence to suggest the form the manifold would take, but if it were folded as in figure 7, then more options would exist for management than if it were not. If the system started in a grassland with low standing biomass, decrease in fire frequency and intensity could cause a shift to forests and high standing biomass at A. If the system started in a forest, increase in fire intensity, at least, could cause a shift to grasslands at B.

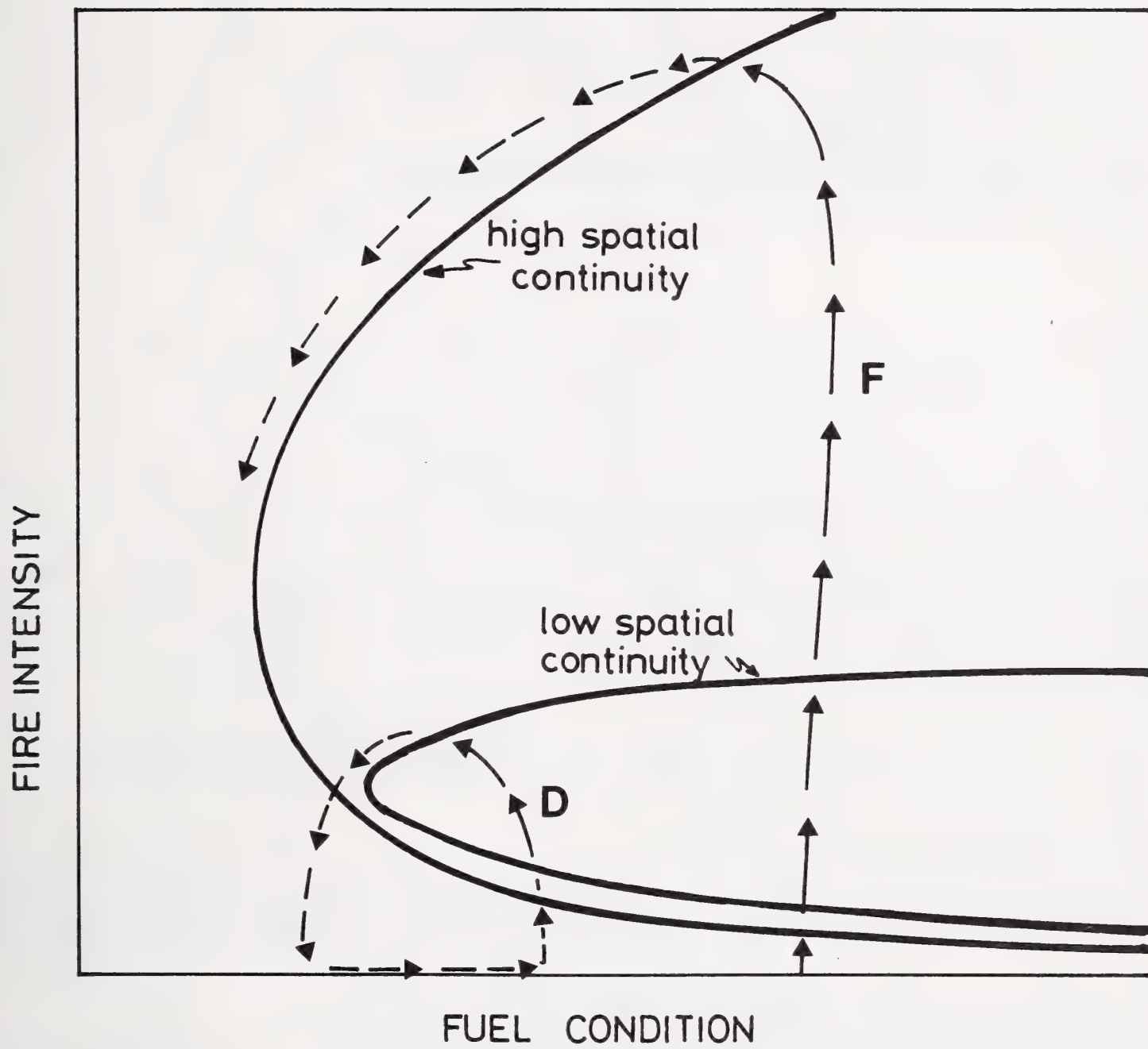


Figure 6.--Equilibrium manifolds under the influence of parameter change.

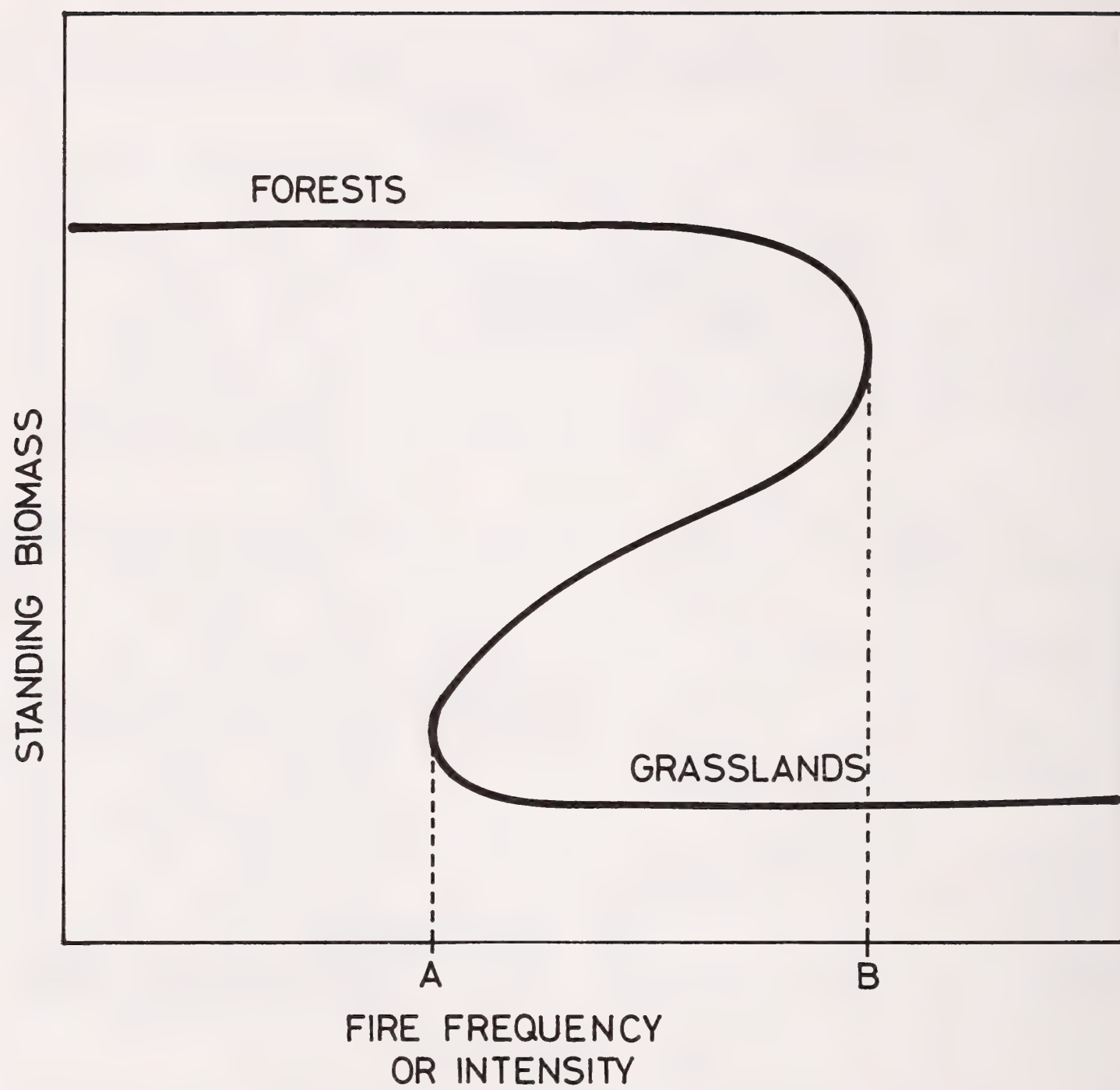


Figure 7.--Hypothetical influence of fire on gross ecosystem properties.

I introduce figure 7 here, in part, to reemphasize the observation from fire studies that ecosystem parameters can shift abruptly when management operates through a control variable like fire frequency and hence intensity. But, in addition, folded structures of this sort have peculiar properties important for the resilience concept. First, they allow each of the two (in this example) distinctly different conditions to exist over a wider range of the control variable than would otherwise be possible. The wider the range of the control variable over which each system can exist, the more resilient it is. Unexpected changes in that variable can be absorbed without major change. Second, in a world of change where objectives can shift, folded structures preserve options more readily. If the goal were to maintain grasslands, the option of shifting to forests could be more effectively achieved by operating within the range A to B. In this range the shift could be made either by reducing the control variable or by adding biomass above the reflexively curved surface. This particular example is trivial because of the ease of controlling fire frequency. But in other systems where the control variable is more difficult to change, the other option for action might more easily be achieved.

In summary, the present analysis of budworm and fire has led to three new insights into resilience. Earlier work emphasized the existence of multiple equilibria in variable and parameter space and the possible significance of variability. (Holling 1973, as reviewed in Peterman and others 1978). The evidence for the existence of multiple equilibria covers terrestrial, aquatic, institutional, and societal systems (Holling 1978). The role of variability in maintaining the stability structure is more speculative, but it suggests that management goals should be less exclusively aimed at producing constancy in one variable. Stability boundaries exist where they are because they are tested. If they are not tested by nature and if they are not otherwise controlled by man, they can shift to produce less tractable problems. This suggests that environmental standards, for example, should not be fixed, but that variables should occasionally be allowed to exceed limits so long as recovery mechanisms that occur naturally are retained, and others are encouraged (Fiering and Holling 1974, Burton and others 1974).

The present paper adds three additional elements to the development of resilience theory:

1. Systems can be in "disequilibrium" not only because of continual external disturbance but because no condition exists where all key variables can be simultaneously at equilibrium. Lacking an equilibrium, such systems are in a state of dynamic disequilibrium, generating high variability.
2. Studies of fire-affected ecosystems demonstrate empirically what was previously deduced. That is, if variability is changed, parameters determining stability domains and equilibria can evolve, sometimes abruptly.
3. Systems with folded multiequilibrium manifolds retain a greater range of attainable options.

Those three developments further confirm that resilience is most concerned with questions of parameter or structural stability rather than local, near-equilibrium notions. Resilience is hence the property of a system to absorb and benefit from change and the unexpected (Holling 1971).

ADAPTING TO SURPRISE

This paper began with the point that success and failure (or surprise) are partners. Surprise is inevitable, and some of its sources have been described in earlier sections. But in some situations there is relatively prompt adaptation to surprise, as in the forest fire management system, and in other situations there is not, as in the budworm control policies of New Brunswick. By comparing the two,

it becomes possible to identify, at least tentatively, some of the ingredients that make adaptability, or learning, either more or less likely.

First, consider the similarities. The original policies, as discussed earlier, were similar. Both were successful for the short term and both failed for similar reasons. Each left a system precariously dependent on increasingly efficient ways to implement the policy. It was necessary to reduce the probability of failure. In each, the cost of failure increased because of the short-term success in reducing the probability of failure. Each is faced with conflicts of public perception. There is great resistance to insecticide use because of past abuses and potential health and environmental hazards. That makes any transition policy to a new kind of management extremely difficult if it employs insecticides. Similarly, the public generally perceives fire as bad. It is likely, for example, that a rigorous application of the Clean Air Act would make new policies of fire management impossible to implement. Finally, both showed at least tactical adaptation: improved insecticides and ways to apply them; improved techniques of fire detection and suppression.

The reasons why strategic adaptation occurred in one situation and not in another must lie in the differences. One of the most important concerns time. Active fire control efforts in U.S. National Parks date to the early 1900's. Moreover, there is an even longer background of experience elsewhere in the U.S. and in Europe. Insecticide control efforts date from the mid-1900's and there was no significant background of earlier experience to draw upon.

But these differences in duration of application have other consequences related to the speed at which the crises became real and perceived. The buildup of fuel is a slow process measured in decades. The buildup of conditions ripe for an extensive budworm outbreak, following control with insecticides, was measured in years. As a consequence, the original parents and advisors to the fire policies were no longer present when the crises emerged. The original parents and advisors are still present in the budworm situation. Changes in policy are more easily achieved by new generations.

The greater speed of appearance of the budworm failure demanded an effective monitoring scheme to give as early warning as possible. There was, in fact, a remarkably extensive and effective effort to continually monitor budworm populations. But there was little effective monitoring of the trees themselves. What monitoring was done greatly exaggerated the health of the forest. Thus, even with observation of spreading budworm populations, there seemed little need to act. The managed forest fire system developed at a more leisurely pace, and it was correctly perceived that fuel, the critical variable, was building up.

Research and developmental differences also occurred. Both generated highly effective and perceptive research efforts leading to a fresh understanding of underlying dynamics. Both improved the technology that was being used. That same technology can be used directly in the new fire management policies. But new technology that is not dependent on insecticides is needed for the new budworm management policies. There was no drive to develop the new policies and hence the new technologies in the face of the initial success.

Finally, the costs and difficulties in shifting to new policies are much less in the forest fire situation than in the budworm situation. In the latter, the geographical scale and the social and economic dependencies are much greater and more complex. Retreat is much more costly.

In summary, then, we can tentatively suggest the following features important in determining an adaptive response:

1. Failures tend not to be perceived until they become crises, but the earlier they are detected the easier is the response.
2. Presumption of success blinds one to detection of error and to the need for further policy analysis and technological development.
3. A climate receptive to change must emerge. That requires:
 - (a) perceptive understanding of the source of surprise;
 - (b) availability of alternative policies;
 - (c) availability of the techniques to implement the policy;
 - (d) time to absorb the new situation and the new understanding; and
 - (e) communication and dialogue among publics.
4. Failure is more easily detected, appreciated, and responded to adaptively if the parents of the original policy have retired.
5. The earlier the problem is detected, the less the cost of change. Hence there is a great need to monitor the correct variables and to develop incentives to respond in the face of inertia and commitments to the past.

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SECTION III

INTEGRATING SUMMARY

Contributors to this section have explored a restricted number of topics within the broad subject of fire in the structure and function of ecosystems. Each has successfully presented stimulating ideas in his individualistic style. Olson provided dramatic quantification of fire as a global process of major biogeochemical dimensions with tabular data and a distributional map for fire for the world. In addition, he devised basic gradients by which ecosystem properties can be examined in a comparative way. The first of these was a graded series of hypothetical carbon balances generated under different fire regimes. The second was a graphic array relating fire intensity with fire impact. From such an array, one might establish coordinates along which other ecosystem properties could be examined, such as the occurrence of symbiotic nitrogen-fixing species, or maximum rates of primary production. It would be interesting to see how rates of net primary production vary through postfire succession over this array, and how the aboveground/belowground biomass ratio changes. Both of these properties are intimately related to the resistance of systems to change by fire, and their resilience in recovery following fire.

Woodmansee conducted a thorough analysis of fire influences on biogeochemical processes with special reference to nitrogen. An emphasis on nitrogen is appropriate because nitrogen is frequently limiting in terrestrial systems, and because it is volatilized to varying degrees upon combustion of fuels. The interacting linkages between fire variables such as temperature and biogeochemical variables such as fuel chemistry are so complex that it is very difficult to make even coarse, cross-system comparisons. It does seem that biological mechanisms for nutrient conservation such as fast regrowth and nutrient uptake are especially effective in systems prone to fire disturbance. In cases where a large proportion of the organic nitrogen pool is lost to volatilization, nitrogen fixers are usually involved in postfire succession. Mechanisms for conserving or recovering chemical resources following fire are ultimately connected with the adaptive traits of species within the system. A collaborative analysis of the evolutionary biology of species in the context of mineral cycling questions might be an interesting and fruitful enterprise.

On youthful terrains or where the substrates are particularly erodable, there can be strong relationships between vegetation and geomorphological processes. These linkages are often reciprocal in nature. Vegetational changes caused by fire can lead to geomorphological events of consequence downstream from the site as well as on the site itself. These geomorphological events can, in turn, influence subsequent vegetational development. Swanson explored such interactions on "worst case" terrains and attempted to relate these cases to ecosystems of lesser geomorphological sensitivity. Swanson underlined the fact that ecosystems exist in a "disturbance complex" in which fire was only one disturbance factor, and emphasized that a holistic analysis required consideration of causal linkages between disturbance factors and their different time scales.

Wright more explicitly reviewed the effects of fire on land-water interactions--the longstanding epitome of spatial relations in ecology. The evidence for chemical effects of burning watersheds on drainages was surprisingly slight, although some of the examples may have been "best cases." On the other hand, there are some cases of extreme particulate transport from burned terrains that need further evaluation. These and postfire influences on the biotic components of stream ecosystems require special attention.

Conversely, aquatic systems can influence the pattern of fire effects on the land. Wright showed how streams and lakes influence the frequency and intensity of fire over the landscape by acting as firebreaks. Certain lakes and bogs are

significant in still another way by providing long-term records of fire history in their sediments.

Holling demonstrated the remarkable analogies between the well-studied spruce-budworm problem of the eastern boreal forest and forest fire management in the West. From these case histories he developed an extremely important point--that some ecosystems will ultimately become decimated by an unusual but eventually certain configuration of natural events and conditions. This generalization has two important applications. First, management strategies that ignore the fundamental instability of particular managed systems will themselves be fundamentally unsound and will ultimately lead to surprises. It is interesting to speculate on the interplay of traditional concepts, bureaucratic dynamics (or the lack thereof), and the occurrence of surprises like this in the evolution of management policy.

The second important consequence of Holling's generalization is its impact on ecological theory. A concept of fundamental instability as a natural characteristic of some ecosystems conflicts with some of our most cherished paradigms. While concepts of succession are now undergoing change, there is still widespread belief that ecosystem development will lead to a stable system--one maintained by evolutionarily derived, homeostatic mechanisms. Developental pathways that lead to the inevitable, dramatic destruction of systems is antithetical to our normal working concepts. Are fundamentally unstable systems common? How can we identify them? One must wonder about the correctness of our paradigms and the extent to which they impede rather than guide our scientific progress. There is an interesting parallel between the role of paradigms in science and concept-based strategies in management--a relationship will made in Holling's paper. Holling also showed how topological analysis may be an analytical and interpretive approach of considerable utility to ecologists and managers involved with a variety of ecosystems, not just those in which fire is a critical issue.

Each of the authors in this section has contributed a number of important ideas to the analysis of fire in the environment. Collectively these ideas represent a rich array of considerations for those who are committed to a holistic analysis of fire-prone ecosystems. What can we do with these ideas?

At a minimum, these papers can serve an anecdotal role for fire ecologists and fire managers by describing interactions that might occur and perhaps should be considered in particular cases. These papers can play a much more important role if more definite, further efforts are to be made to gain a holistic view of fire. These papers could be a useful starting point for serious assessments of the total consequences of fire regimes in the near and long term. For example, it would seem feasible and useful for a team of experts in a particular ecosystem type, such as California chaparral, to utilize the ideas in these papers towards the development of a nonmathematical model of fire in the chaparral system. Even the simplest of diagrammatic models like a causal loop model would be useful by forcing the considerations of relationships between all ecosystem components, and would naturally lead to a recognition of what knowledge was most badly needed.

Nature often seems inscrutable in its infinite variety and complexity. For this, those who enjoy the intellectual exercise of achieving understanding may rejoice, for the game is never ending. On the other hand, we must achieve a much higher degree of understanding for the intelligent management of our resources. From this point of view, nature's inscrutability is a very serious challenge. As demonstrated by papers in this volume, a gratifying measure of understanding has been gained. Ecosystem analysis can make important contributions to furthering these goals by its organizational process and holistic perspective. An exciting prospect of intellectually rewarding and practically significant enterprise lies before us.

William A. Reiners

SECTION IV

FIRE POLICY AND ECOSYSTEM MANAGEMENT

This section deals with how fire policy and its implementation are influenced by basic research. Unfortunately, meetings between research scientists and resource managers do not often achieve the significance they should in changing ecosystem management policies. Why is this so? Managers are under pressure to make decisions on how to produce a myriad of goods and services from forest and range ecosystems while protecting these ecosystems from degradation. Hence, land managers are extremely interested in quantifying what is needed from an ecosystem and how it might respond to management practices. Even though there is an urgent need for fundamental knowledge necessary to make sound management decisions, research scientists publish their conclusions, for the most part, in a manner no different from scientists 100, 200, or more years ago, and the person on the ground--the practitioner--has to dig the information out of volumes of published literature. Therefore, the problem is in part how research scientists present their conclusions and information. What we examine in this section is how basic research is used by managers as well as how social and economic concerns force changes in management practices.

Specifically, we will examine how fire is used to maintain natural ecosystems, how it is used to meet specific land management objectives, and how fire cycles have been altered by suppression activities. We will also examine some regional impacts of fire and what off-site effects mean to fire management programs. We will look at current fire policy in the USDA Forest Service and some thoughts on how it came to be. Finally, we will examine an age-old land management practice in the tropics, what its implications are today, and how social and economic considerations influence land management practices. These papers illustrate how fire management policies are changing and that scientific information is important in effecting these changes.

James E. Lotan



THE ROLE OF FIRE MANAGEMENT IN MAINTAINING NATURAL ECOSYSTEMS

David J. Parsons

Research Scientist
Sequoia and Kings Canyon National Parks
Three Rivers, California

ABSTRACT

Fire, both naturally ignited and man caused, has long played a role in the evolution of many of the world's natural ecosystems. During the past century, fire has often come to be regarded as a destructive force, leading to efforts to eliminate it as an important ecological factor. Yet, if naturally functioning ecosystems are to be maintained, fire must be allowed to play its primeval role. A growing understanding of this necessity in recent years has led to the implementation of integrated fire management programs in many areas. These programs may utilize both lightning-ignited and/or intentionally set or prescribed fires to achieve carefully predetermined resource management objectives. This paper discusses the current status of fire management as well as the background information needed to formulate and implement an integrated fire management program.

KEYWORDS: fire management, prescribed burning, natural fire frequency, preservation, role of fire and land use planning.

INTRODUCTION

Fire has played an important role in the evolution of natural ecosystems throughout the world. Whether ignited intentionally or by natural causes fire has periodically burned forests, brushlands, and grasslands for thousands of years (Stewart 1956). Varying fire frequencies and intensities have helped to determine the structure and distribution of many of the world's plant and animal communities. In fact, many natural communities depend on periodic fire for their survival. When fire is excluded from such areas, changes in successional patterns and thus species composition generally follow. Without periodic fire we can expect, and in some cases have actually observed, major changes in much of the world's natural landscape.

In recognition of the vital role fire plays in maintaining natural ecosystems, its use is now accepted as a necessary tool for the management of many natural areas (Kilgore 1976, Parsons 1977). Today's land manager is increasingly faced with the challenge of developing and implementing resource management programs which include the use of prescribed burning as well as naturally ignited fire.

"Fire management" is a relatively new concept which has had considerable impact on natural resource management programs in recent years. While many definitions of fire management have been proposed (Sando 1978), in the present context I will use that of Barney (1975): "The integrating of fire-related biological, ecological, physical, and technological information into land management to meet desired objectives." In such a discussion it is important to distinguish between using fire to achieve the objective of maintaining natural ecosystems and using fire as tool to favor particular plant or animal species.

THE ROLE OF FIRE IN THE PRESERVATION OF NATURAL ECOSYSTEMS

The need to preserve large areas as naturally functioning ecosystems, apart from the influences of modernized society, has been of growing concern throughout the world. The ever increasing number of National and State Parks, Wilderness Areas, biosphere reserves, and nature preserves attest to a recognition of the need to protect examples of undisturbed biotic communities (Dasmann 1972, Franklin 1977).

The traditional approach to the preservation of natural areas has involved the complete protection of all biotic and abiotic resources. Such a policy generally included attempts to eliminate fire. For example, in the United States the policy of suppressing fires in National Parks began in Yellowstone National Park in 1886 and was implicitly incorporated into the official policy of the National Park Service in 1916 (Agee 1974). A similar policy has long been in effect for most of the Nation's National Forests (Mutch 1977) and in vegetated areas throughout the world (Owen 1972, Naveh 1974). Fire exclusion was justified on the basis that fire removes nutrients, promotes floods and erosion, and destroys trees and brush, thus removing forage as well as destroying breeding habitat for birds and wildlife (Kilgore 1976).

Recognition of Fire's Role

HISTORICAL EVIDENCE

Man has recognized the value of using and controlling fire for between a quarter and a half million years (Stewart 1956). Early man deliberately set fire to wide expanses of vegetation in order to improve hunting and food gathering as well as facilitate passage through dense forests or brush. He recognized the value of fire, both intentional and naturally ignited, in thinning the forest, reducing ground fuels, improving forage, and stimulating the growth of many plant species. In more recent times fire has continued to be widely utilized as a tool to modify vegetation (Kayll 1974). For example, intentional burning by Indians is known to have been common throughout much of the western United States (Lewis 1973). Early European settlers continued these burning practices (Heinselman 1978). Historical accounts of man's use of fire, together with his early recognition of its beneficial effects on vegetation and wildlife (Stewart 1956), reveal a long standing appreciation of fire both as a management tool and as an important ecological process.

During the past century modern man has lost much of his understanding of the natural role of fire. Catastrophic wildfires in the late 19th and early 20th centuries led to fire becoming regarded as a destroyer which was to be avoided at all cost (Lotan 1979). In an attempt to eliminate destructive wildfires the benefits derived from periodic burning were overlooked. Only in the last few years has man again begun to appreciate fire as an important natural process.

Even without man's help, fire would be a common occurrence throughout much of the world. Lightning, the chief cause of natural ignitions in most areas, has long been recognized as a common cause of wildland fires (Komarek 1967). Numerous ecological studies have documented that lightning has always been a major cause of fire in most forests (Taylor 1971), grasslands (Vogl 1974), and brushlands (Biswell 1974, Vogl 1977) of North America. Similar evidence is available to document the importance of lightning fires in such areas as Australia (Gill 1975), Africa (Phillips 1974), and the Mediterranean Basin (Naveh 1974). Volcanoes are the only other source of natural ignition which are thought to have influenced significant areas of native vegetation (Stewart 1956, Phillips 1974). In recent years studies utilizing fire scars (Arno 1976, Kilgore and Taylor 1979) and lake sediments (Swain 1973) have helped to document the historical frequency of fire in selected community types.

BIOLOGICAL EVIDENCE

Scientific investigations into the role of fire as a natural process have provided a sound biological basis for understanding its impact on plant and animal communities throughout the world (Kozlowski and Ahlgren 1974, Gill 1975, Mooney and Conrad 1977). The adaptations of many plant species to fire provide strong support that fire has long been an integral part of most natural ecosystems. Typical fire adaptations include regeneration by stump or branch sprouting or by rooting of underground stems (Biswell 1974, Gill 1977), production of large numbers of seeds (Keeley and Zedler 1978), the ability of seeds to remain dormant and viable in the soil for long periods (Biswell 1974), and the need for some seeds to be heat scarified in order to germinate (Gill 1977). Other species possess serotinous cones which open only after high temperatures (Lotan 1976) or fire-resistant bark (Hartesveldt and others 1975) or foliage (Daubenmire 1974).

When looked at on the community level, fire plays several functions which support the concept that it is essential to the perpetuation of many ecosystems. For example, fire is known to (1) prepare seedbeds, (2) adjust the successional pattern, (3) influence the mosaic of age classes and vegetation types, (4) control plant community composition, (5) regulate the amount and type of fuel accumulation, (6) recycle nutrients, (7) increase or decrease forest insects and disease problems, and (8) directly influence wildlife habitat (Kilgore 1973, Parmeter 1977, Heinzelman 1978). Furthermore, Mutch (1970) has hypothesized that plant species that have survived tens of thousands of years of fire may have undergone selection for structural or chemical characteristics which make them more flammable. Such properties would contribute to the perpetuation of fire-dependent plant communities.

The impacts of fire on wildlife are commonly overlooked since they most often act indirectly through changes in the vegetation. Nevertheless, recent studies are available to document the dependence of major wildlife species on periodic fire (Loope and Gruell 1973, Bendell 1974, Koehler and Hornocker 1977, Walter 1977). The fact that one or more fire adaptations can be found in almost all of the world's major ecosystems provides strong support for fire having been an important factor in the evolution of most natural communities.

IMPACT OF RECENT FIRE SUPPRESSION

The fire suppression programs which have been common in many areas over the past century or more have had a considerable impact on natural ecosystems. Besides the altering of successional trends and nutrient cycling, the era of fire suppression has no doubt altered vegetative mosaics as well as the natural functioning of wildlife, insect, and disease populations.

One of the more significant impacts of continued fire suppression has been the buildup of flammable fuels (Dodge 1972). When fire is artificially excluded from an area accustomed to frequent burning, there follows an unnatural buildup of both live and dead fuels. This eventually may increase the chance of an unnaturally hot, often highly destructive wildfire. In the mixed conifer forests of the Sierra Nevada, the buildup and rearrangement of both ground and aerial fuels under a policy of fire exclusion have been of special concern. For example, Kilgore and Sando (1975) have shown how the increase of shade-tolerant understory trees in a giant sequoia (Sequoiadendron giganteum) forest increases the chances of destructive crown fires.

The mounting accumulation of forest fuels has also had the discouraging effect of requiring a continually more sophisticated level of fire suppression. Such a policy is extremely expensive and may serve only to delay the inevitable destructive wildfire. At least in the case of natural areas, the careful reintroduction of fire to its historical role appears to be the only way to escape from this cycle.

EVOLUTION OF FIRE MANAGEMENT POLICY

Given the overwhelming evidence in favor of the need to include fire as a vital process in the preservation of natural ecosystems, it is hardly surprising that the policy of suppressing all wildland fires has been increasingly challenged in recent years. It is no longer acceptable for land managers to merely "protect" wildland resources. It is increasingly important that they recognize and fully understand fire as an important ecosystem process.

Early Challenges to Fire Suppression

The first serious challenges to the policy of total fire suppression came from the southeastern United States (Kilgore 1976). Early studies on the impact of periodic fire on southern pine forests led to adoption of a limited prescribed burning policy in 1943. This soon led to broadcast surface fires in several southern forests. By this time early investigations were also being made into the role of fire in the western United States. These studies included experiments with prescribed burning in ponderosa pine (Pinus ponderosa) forests which concluded that this vegetation type evolved with frequent low-intensity surface fires and that fire exclusion had halted many natural processes as well as creating extreme fire hazards (Weaver 1974). Despite evidence for the important role fire played in ponderosa pine forests, there continued to be considerable resistance on the part of Government agencies and private interest groups to any change in the existing suppression policy.

Recent Policy Changes

In 1963 the Leopold Report (Leopold and others 1963) on wildlife management in National Parks addressed the types of changes which have occurred with the elimination of fire from National Park lands. Specifically discussing conditions in the Sierra Nevada of California the report stated "...much of the west slope is a doghair thicket of young pines, white fir, incense-cedar, and mature brush - a direct function of over-protection from natural ground fire." The report suggested that by "using the utmost in skill, judgment, and ecologic sensitivity" it should be a goal of the National Park Service to restore fire to its natural role in this area. The Leopold Report was largely adopted as National Park Service Policy in 1968. This symbolized the beginning of a dramatic change in attitudes toward fire suppression.

Present National Park Service fire management policy recognizes the importance of fire as a natural process. It allows for the use of fire, either naturally ignited or man caused, under carefully prescribed conditions to achieve land management objectives. In National Park Service natural areas, such objectives are based upon the maintenance of naturally functioning ecosystems.

While the USDA Forest Service may have, at first, been more cautious in accepting this new fire management philosophy, considerable progress has been made in recent years. Beginning in 1972, several exceptions to the well-established "10 a.m. Fire Suppression Policy" which called for aggressive suppression action aimed at control of all fires by 10 a.m. of the following day were authorized. And finally, as of February 1978, the "10 a.m. policy" was revised to provide more flexible policy calling for well-planned integrated fire protection and fire use programs that are responsive to resource management objectives (Lotan 1979). Today, fire management plans which call for the use of natural fire under prescribed conditions currently exist or are being prepared for areas in many National Forests. Such plans emphasize the importance of integrating natural fire management with the continuation of a highly aggressive suppression capability (Mutch 1977).

Such changes in fire management policy represent a successful transition from total fire control to a policy of utilizing fire as a tool in perpetuating natural communities. Such a transition requires the intricate weaving of principles of fire ecology into day-to-day management programs.

Fire Management Alternatives

Once it is determined that fire is a necessary tool to maintain or reestablish natural communities of an area, consideration must be given as to what kind of fire management program will be utilized. Fire management may include the use of naturally ignited fire, as well as fires which are intentionally set to achieve specific management objectives. The latter is most commonly referred to as prescribed burning. In either case, an active fire suppression program may also be needed.

The ideal way to restore fire to its natural role would be to allow all lightning or other naturally ignited fires to run their course. In those areas which have been little affected by fire suppression activities, such as higher elevation communities where growth is slow and thus rates of fuel accumulation are low, naturally ignited fires often can be allowed to burn so long as they meet predetermined prescriptions and remain within established boundaries. Prescriptions, which are the conditions under which a fire is allowed to burn, must be established separately for each area. They may limit the program to certain times of the year or to specified weather conditions. Constant surveillance and monitoring of all such fires is required. With few exceptions man-caused fires are generally suppressed in natural fire management zones.

In many areas the era of fire suppression has resulted in levels of fuel accumulation which would produce unnaturally hot fires were natural ignitions allowed to burn (Kilgore and Sando 1975). In other areas, historical structures and other manmade developments might be threatened. In such cases, it has proven desirable to use intentionally set, prescribed fire under predetermined weather and fuel conditions. Such fires may be used either to simulate natural fire or to reduce unnatural fuel accumulations and return the affected ecosystems to the condition they would be in had fire suppression activities not taken place. In either case, prescribed burning is a highly sophisticated art which should be conducted only under selective conditions.

Where private property, human life, or developments might be threatened or where past fire suppression activities have resulted in such large fuel buildups that fires would burn unusually hot, it is important that all unplanned fires be extinguished

immediately. Effective fire suppression is also necessary whenever natural or prescribed fires exceed preestablished prescriptions as well as for most accidental or arson-caused fires. Thus, it is important that all fire management plans include provisions for fast, effective suppression capabilities. Furthermore, it should be emphasized that despite integrated fire management it is important that the "Smokey the Bear" philosophy of preventing all unplanned, man-caused fires be continued.

Existing Fire Management Programs

While most Federal, State, and local land management agencies have long had some type of fire suppression program, to date only the National Park Service and USDA Forest Service have adopted a fire management policy which includes the use of fire to maintain natural ecosystems. Details of individual programs, which may include the use of natural fire and/or prescribed burning, depend to a large extent on vegetation type and past fire history.

The first place where naturally ignited fires were allowed to burn was within a high-elevation zone of Sequoia and Kings Canyon National Parks (Kilgore and Briggs 1972). Since the program's inception in 1968, 151 naturally ignited fires have burned nearly 8 000 ha in the upper mixed conifer, subalpine, and alpine zones of these Parks (table 1). While 75 percent of the fires have remained under 0.1 ha in size, three have burned over 1 000 ha each, with the largest being 4 048 ha. These fires occurred primarily in lodgepole pine (*Pinus contorta* var. *murrayana*), white fir (*Abies concolor*), and Jeffrey pine (*Pinus jeffreyi*) forests between 2 100 m and 2 800 m in elevation. They were all ignited by lightning during dry summer months and burned until being extinguished by winter snows. Each fire was characterized as a slow-burning, low-intensity ground fire which rarely burned into the tree canopy. Rock outcrops, ridges, and other areas of sparse vegetation formed natural fire-breaks which slowed the fire's progress. Research and monitoring activities have been carried out in conjunction with the larger fires (Parsons 1977).

More recently, a number of other National Park Service areas have implemented natural fire management programs aimed at restoring fire more closely to its natural role. As of late 1978, 12 areas have zones within which naturally ignited fires are allowed to burn (table 2). While specific guidelines or allowable prescriptions may differ between areas (for example, Everglades National Park allows some man-caused fires to burn if they achieve management objectives), as of October 1978 a total of 536 natural fires have burned approximately 20 986 ha in 12 National Parks and Monuments. At least five additional Park Service areas are currently planning natural fire management programs.

While natural fire is the preferred way to restore fire to a community, it is not always possible to do so. Heavy fuel accumulations or proximity of private lands or developed areas may prohibit allowing natural fires to burn. For this reason a number of National Parks and Monuments have active prescribed burning programs. Generally, the objectives of such programs are either to simulate the effects of natural fire or to reduce unnatural fuel buildups to such a level that natural fires can again be allowed to burn. Especially active prescribed burning programs are underway in Everglades, Sequoia and Kings Canyon, and Yosemite National Parks. Everglades National Park first embarked on an experimental prescribed burning program in 1958. In 1972, this was expanded into a fire management program which integrated the use of naturally ignited fire and prescribed burning in an effort to preserve the Park's natural communities. The prescribed burning portion of the program is now aimed primarily at simulating the role of natural fire in favoring pine over hardwoods, reducing fuel hazards, and controlling exotic plants (Bancroft 1976). In Sequoia and Kings Canyon and Yosemite National Parks, prescribed burning programs have been underway since 1968 and 1970, respectively. The objectives of these programs are to reduce

TABLE 1.--Natural and prescribed fires, by year, Sequoia and Kings Canyon National Parks.

Year	Natural fires		Prescribed burns	
	No.	ha	No.	ha
1968	2	3.2	1	323.9
1969	2	0.1	3	2,566.8
1970	24	200.0	2	526.3
1971	19	57.3	2	43.6
1972	16	65.5	6	959.1
1973	11	1,932.2	0	0.0
1974	19	1,340.8	2	135.2
1975	7	23.6	1	13.4
1976	20	31.3	10	110.1
1977	9	4,312.1	14	298.4
1978	<u>22</u>	<u>2.4</u>	<u>5</u>	<u>152.3</u>
Total	151	7,968.5	46	5,129.2

TABLE 2.--National Parks and Monuments with natural fire programs, 1968-1978

Area	Year of implementation	Size of natural fire zone	Total No. fires	Total area burned
		ha		ha
Sequoia and Kings Canyon	1968	242,892	151	7,969
Saguaro	1971	22,672	40	370
Everglades	1972	285,456	87	6,252
Grand Teton	1972	59,109	14	1,508
North Cascades	1972	234,818	1	10
Yellowstone	1972	688,259	49	971
Yosemite	1972	288,758	165	3,283
Rocky Mountain	1973	94,332	7	401
Crater Lake	1978	44,864	6	219
Glacier	1978	40,486	0	0
Grand Canyon	1978	435,893	12	3
Hawaii Volcanoes	1978	<u>38,988</u>	<u>0</u>	<u>0</u>
Total		2,416,527	536	20,986

fuel accumulations and return the natural ecosystems to the condition they would be in today had fire suppression activities not taken place. Details of each of these programs have been discussed by Schuft (1973), Parsons (1977), and van Wagtendonk (1977). As an example, table 1 presents the number and size of prescribed burns for each year since 1968 in Sequoia and Kings Canyon National Parks. The large acreage burned during early years of the program reflects a reaction to the Leopold Report and the 1968 shift in Park Service policy. In recent years the program has focused more on refining prescriptions and accomplishing specific objectives than on burning large areas. It is anticipated that, given sufficient funding, the availability of considerable background data should allow for a greatly expanded prescribed burning program during the coming years.

The Forest Service first approved the use of natural fire as a land management tool with the approval of the 26 720 ha White Cap Fire Management Area in the Selway-Bitterroot Wilderness of Idaho in 1972. Fire management prescriptions for the area were determined on the basis of wildland fuels, plant communities, landforms, and fire spread and intensity potentials (Mutch 1974). The plan allows different management strategies in different habitat types. In 1973 a lightning ignition in the ponderosa pine-savanna fire management zone burned a total of 500 ha before being extinguished by rain. The fire proved to be a success from both the management and scientific points of view (Daniels 1974, Mutch 1974). This area in which natural fires would be allowed to burn was more than doubled in size with the approval of the adjacent Bear Creek fire management area on the Nezperce National Forest in 1974. These areas were both included in larger fire management areas in 1978. One or more lightning fires have been allowed to burn within the Selway-Bitterroot Wilderness in all but one year since 1972.

As of January 1976, additional natural fire management areas had been approved in the Gila Wilderness in New Mexico, the Teton Wilderness in Wyoming, and in two National Forests in the south (known as the DESCON program, Designated Control). The Teton Wilderness fire plan is unique in that a cooperative agreement with adjacent Yellowstone National Park allows for natural fires to move across administrative boundaries in either direction as long as they meet the receiving area's prescriptions (Chapman 1977). A similar agreement with Grand Teton National Park as well as proposed agreements with two adjacent forests promise to make this area the largest designated natural fire management area in the country. It is anticipated that over 700 000 ha of Federal land may eventually be included within this natural fire area. Chapman (1977), has documented the decisionmaking process as well as recent fire history for the Teton fire management area.

The DESCON program is unique in that it allows for the use of benign wildfires to achieve land management objectives (Devet 1976). It differs from other natural fire programs in that if a wildfire, regardless of cause, falls within predetermined prescriptions and meets a decision-logic table process (Devet 1976) it is declared a prescribed fire and managed accordingly. This may involve additional firing and/or line building. Decisions on whether to declare a fire DESCON are based on potential fire behavior, potential for achieving desired objectives, and cost considerations. Since its beginning in 1973, 25 DESCON fires have burned 2 599 ha in the Francis Marion National Forest in South Carolina while two fires have been allowed to burn 19 acres on the Kistachie National Forest in Louisiana.

Since the policy revisions of early 1978, there has been a rapid change in the natural fire management program of the Forest Service. A number of new fire management areas were approved in time for the 1978 fire season, greatly expanding the area in which natural fires are allowed to burn. Numerous additional plans are now being prepared for the 1979 season. For example, in the Intermountain Region, which includes Utah, Idaho, and Wyoming, there were nine approved and 14 proposed fire management areas as of September 1978. While not all of these are specifically designed to allow

for natural fires, the rapid proliferation of areas does reflect a revised attitude towards fire management. It is anticipated that eventually most, if not all, designated wilderness areas as well as selected nonwilderness areas will include natural fire management areas.

While to date prescribed burning has not been widely accepted as a tool for perpetuating natural communities in Forest Service areas, outside the southeast, there is some indication that it may soon play an expanding role to help meet resource management objectives (Mutch 1977).

Most other Federal, State, and local agencies are still oriented toward fire suppression activities (Phillips 1977). Nevertheless, there is evidence of growing interest in accepting and using fire as natural part of the environment. For example, the Bureau of Land Management recognizes the importance of understanding the natural role of fire and has shown recent signs of adopting a more progressive fire management policy (Wilson 1977). State and local governments are likewise adopting the use of fire as a management tool for maintaining natural communities in many areas. For example, in Calaveras Big Trees State Park in California, a prescribed burning program is underway in an effort to perpetuate giant sequoia (Biswell, personal communication), while in Itasca State Park in Minnesota, extensive data on fire history have provided the background necessary for implementation of a similar program (Frissell 1973).

With the exception of Australia and parts of Africa, where prescribed burning of wildland vegetation has been utilized in part to perpetuate native communities for many years (Hodgson 1967, Phillips 1974), there is little evidence of other countries showing interest in implementing fire management programs for the purpose of maintaining naturally functioning ecosystems. Even in instances where it is now understood that periodic fire is essential to the perpetuation of a vegetation type (Liacos 1974) there is a hesitation to adopt an intentional burning program.

In such areas as Alaska, northern Canada, and parts of Australia where lightning ignited fires are often allowed to burn, it is usually because suppression would be too difficult and expensive. Groves (1977), for instance, states that despite an extensive and successful prescribed fire program, land managers in Australia are not yet ready to accept a policy of allowing natural fires to burn. Few other countries have yet to even consider such a possibility.

DEVELOPMENT OF A FIRE MANAGEMENT PROGRAM

Analysis of information needed to develop a fire management program points out many important questions faced by today's land manager. As a first step it is important to identify the program's objectives. For example, where the desire is to maintain or restore naturally functioning communities the primary objective might be "to restore fire to its natural role in the ecosystem." In such cases the reduction of ground fuels or the creation of specific mixes of species or vegetation types might serve as short-term goals of individual prescribed burns. Such burns would help return the area to a condition under which naturally ignited fires could again be allowed. In other instances, objectives of a fire management program might specifically include fuel reduction or improvement of conditions for wildlife.

The Fire Management Plan

The development of a fire management plan is an important prerequisite to any active program. The plan should incorporate all available background data into a working document. Besides a detailed description of soils, topography, vegetation, and wildlife of the area, the plan should address what is known of the role and past frequency of fire in each community type. As well as discussing objectives

of individual burns, the plan should identify the type of ignition and prescriptions to be used within the planning area. Monitoring and research needs as well as potential conflicts with the program should also be addressed. The plan should provide for an orderly means of implementation, including the preparation of specific burn plans for anticipated prescribed burns (Fischer 1978). Finally, a fire management plan must address the condition for, and means of, effective suppression action.

Historical Data

NATURAL ROLE OF FIRE

Before a plan can be developed for the use of fire to maintain natural ecosystems, it is essential to understand the historical role of fire in the area of concern. Such information should include causes, size, frequency, intensity, and seasonal and geographic distribution of past fires. The periodicity of repeat burning and extent and impact of recent fire suppression activities on the natural fuels and vegetative mosaics should also be understood. To the extent possible, such data might be derived from historical literature together with studies of local vegetation, topography, and climatic conditions. When the necessary information is not available, inferences must be made from other areas with similar natural fire regimes.

The frequency and intensity of the fires under which an ecosystem evolved constitute its natural fire regime. For example, Sando (1978) has identified four major natural fire regimes in North America. They are respectively characterized by (1) frequent fires of low to moderate intensity, (2) infrequent fires of high intensity, (3) frequent fires of high intensity, and (4) infrequent fires of low to moderate intensity. Each regime has its characteristic vegetation types as well as fire adaptations and fuel and land management problems. Information derived from one area should be at least partially applicable to other areas within the same regime.

The problem of distinguishing between past lightning ignitions and man-caused ignitions can be simplified somewhat by considering all presettlement activities as part of the natural scene (Kilgore 1973, Heinselman 1978). Thus in the United States fires started by pre-European man are considered as part of the natural fire regime. This commonly used definition is supported by evidence that in many areas lightning either continues to account for most of the area burned or that early man merely served as an alternate ignition source (Heinselman 1973, 1978). In the United States the impact of exploration and settlement in the 18th and 19th centuries served to either increase or decrease the natural fire frequency depending on the area in question (Loope and Gruell 1973). While it is generally assumed that more recent improvement in fire suppression techniques has decreased the natural fire frequency (Houston 1973), Keeley (1977) has shown that recent man-caused ignitions have actually increased the number and size of fires in some areas.

PAST FIRE FREQUENCY

The past fire frequency of an area needs to be understood before an effective fire management program can be developed. Such information provides the basis for evaluating whether naturally ignited fires occur often enough to simulate past frequencies or whether they need to be supplemented with intentional ignitions. In a prescribed burning program, data on past fire frequency enables the manager to set fires to approximate the natural frequency including the option of replacing any fires lost by the cessation of Indian burning.

Analysis of fire scars has proven to be a valuable tool for reconstructing fire histories in the coniferous forests of the western United States. Kilgore and Taylor (1979) have used scars on cross sections of fir and pine to trace over 400 years of fire history in a sequoia-mixed conifer forest in the southern Sierra Nevada of California. Their data are especially useful for evaluating the impact of European

settlement on natural fire frequency. It should prove of great value in the development of natural and prescribed fire programs in that part of the country. Arno (1976) has utilized similar techniques in a study of the historical role of fire in northern Rocky Mountain forests. In recognition of the value of such techniques, Arno and Sneek (1977) have recently provided a well-documented methodology for using scars to determine fire histories in coniferous forests. In addition to documenting fire frequencies, such techniques have proven of value in determining sizes and intensities of past fires (Houston 1973, Kilgore and Taylor 1979).

In areas where intense crown fires commonly kill most or all of the aboveground vegetation, increment borers may be utilized to document the date of the most recent fire but would be of little use for dating earlier fires. Similarly, fire scar techniques are of little value in areas where trees do not produce annual rings or in areas dominated by brush or herbaceous vegetation. Other methods which have been effectively used to determine past fire frequencies include stand age (van Wagner 1978), and dating of charcoal deposits in lake and ocean sediments (Swain 1973, Byrne and others 1977). Written accounts of explorers, early settlers, and historians are often useful in evaluating recent fire histories. Compilation of available data from each of these sources together with findings from any new studies which might be needed provide the manager with background information needed to identify natural fire frequencies.

IMPACT ON VEGETATION

An understanding of how fire history affects vegetation structure and composition provides a basis for evaluating the impact of alternative fire management strategies. For example, if there has been a recent change in the fire history of an area, such as that caused by suppression policies, it is important to know how this has influenced the native vegetation. Such information is also of value in predicting impacts of future fire management actions.

Several investigators have utilized age of standing woody vegetation and dead plant material to reconstruct changes in species composition in forest communities (Henry and Swan 1974, Oliver and Stephens 1977, Parsons and DeBenedetti 1979). Ongoing studies by Stone and Bonnicksen (unpublished data) utilize the concept that forests reproduce in small, homogeneous vegetation units or aggregations to describe past as well as predict future successional changes in a mixed conifer forest. They feel these techniques will prove of great value in reconstructing past forest structure, thus providing a picture of what park managers should attempt to recreate. Swain (1973) has successfully used pollen analysis to document long-term vegetation change in relation to fire history. Such techniques should help provide the basis necessary to extend knowledge of vegetation structure back hundreds and, perhaps, thousands of years.

Fuels and Vegetation Data

One of the first steps in developing a fire management program is to inventory existing vegetation and ground fuels. The density, composition, and structure of standing biomass together with amount and configuration of dead surface fuels are of primary importance in predicting the intensity and behavior of future fires (Kilgore and Sando 1975, Philpot 1977).

In addition to standardized sampling techniques, recent advances in fire research have provided specialized procedures for evaluating wildland fuels as well as predicting the impact of fire on plant and animal communities. Kessell (1976) has utilized gradient models of living vegetation, ground fuels, and wildlife distribution as a basis for predicting fire behavior and postfire succession. In addition to providing a basis for evaluating the immediate impact of a fire on a specific area or on selected species, Kessell's gradient model can help predict long-term changes.

An understanding of the physical and structural aspects of wildland fuels provides an effective basis for predicting fire behavior (Deeming and others 1977). Successful methods of evaluating fire fuels include keys for appraising forest and brush fuels (Fahnestock 1970) and a line intercept method of inventorying downed woody material (Brown 1974). Litter and duff material can be effectively sampled by direct collection and weighing or through the development of regression correlations between fuel depth and fuel weight (Agee 1973). A variety of mathematical models are now available which utilize such data to predict rate of spread and fire intensity. For example, Rothermel and Philpot (1973) have used fuel loading for live and dead material, including surface-area-to-volume ratio, size class, heat content, and fuel moisture to predict changes in flammability and rate of spread for California chaparral.

Development of Prescriptions

The conditions or prescription under which fires will be allowed to burn must be carefully defined for both prescribed and natural fire programs. In all cases these must include the protection of threatened and endangered species, cultural and historical structures, and safety of visitors. Assurances must be made that fires will not be so intense as to threaten the survival of the very resources being protected. Prescriptions commonly include confinement to above a certain elevation or within predetermined boundaries, limitation to certain times of the year or only after specified weather conditions have been met (van Wagtendonk 1977). For example, in formulating the White Cap Fire Management Area, a specified Buildup Index, reflecting level of dryness, was used as a prerequisite for allowing a naturally ignited fire to burn (Mutch 1974). Continual refinement of such prescriptions, which of course should start on the conservative side, can be achieved through fuels inventories, observation of fire behavior in relation to fuels and weather conditions, and monitoring of short- and long-term impacts of fires which do occur.

In planning for prescribed burns with deliberate ignition, it is especially important that burning prescriptions be established. These will most often include such factors as air temperature, windspeed, relative humidity, and fuel moisture and are commonly expressed in terms of the variables in the National Fire-Danger Rating System (Deeming and others 1977). Acceptable ranges in values of these variables, which are expressed in such terms as Ignition Component, Spread Component, and Burning Index, have been determined for a number of well-defined fuel models (Deeming and others 1977). Other types of prescriptions have been successfully used in different habitats. For example, the two most important parameters of fire prescriptions in Everglades National Park have been drought index and soil moisture (Bancroft 1976).

In order to extend established prescriptions into other vegetation types, experimental burns should be monitored for weather and fuel conditions, fire behavior, and fire effects. Van Wagtendonk (1974) has successfully used such experimental techniques to refine burning prescriptions for the various mixed conifer forest types of Yosemite National Park.

Computer Models

In recent years successful use of computer models to predict fire behavior and effects has provided a tool of potential value in all fire management programs. Rothermel (1972) has developed a widely used mathematical model for predicting rate of fire spread and intensity for a wide range of wildland fuels. The major weakness of this model has been the necessary assumption of a uniform spatial distribution of fuels. This problem was partially solved by developing a multistrata fuel model (Kessell 1976). This refined fire behavior model has recently been combined with gradient models of vegetation, microclimate, and fuel moisture to develop a fire management system for Glacier National Park (Kessell 1976). The model predicts fire behavior (rate of spread, fireline intensity, flame length, and scorch height) and fire's

potential effects on vegetation and fuel succession. A similar computerized fire behavior information system has recently been developed and utilized for the southern California chaparral (Kessell and others 1977). A more recent Forest Planning Language and Simulator (FORPLAN) has been developed for integrating fire considerations into multiple-use land management planning by the USDA Forest Service (Kessell and others 1977, Potter and others 1979). That system combines numerous models and data bases into a single system, models fire behavior and effects, and predicts ecological effects of thinning and timber harvesting activities. FORPLAN is also readily accessible to the manager without computer training as it is programed in common English words and phrases. There is every indication that computer models of fire behavior and subsequent effects on fuels, vegetation, and wildlife will soon become a vital part of all successful fire management programs.

Monitoring and Research Needs

In addition to basic monitoring of the effects of management fires on vegetation and fuels, it is important that pre- and postburn monitoring of wildlife, disease organisms, and water and air quality be incorporated into all fire management programs. To effectively compare the impact of different prescriptions, burning techniques, or fires in different community types, it is desirable that a standardized measure of intensity be calculated for all management fires. Fire intensity may be calculated from the equation:

$$I = HWR$$

where I is fire intensity, H is the heat or energy value of the fuel, W is the weight of fuel consumed per unit area, and R is the rate of spread. In this sense intensity is a measure of the energy released per unit of fire front and time, and is expressed in kilocalories or joules per second per meter (van Wagtendonk 1974). Such a standardized measure provides a much needed basis for comparing management fires in different areas and under different conditions. More recently flame length has been utilized as an easily quantifiable measure of intensity by many fire behaviorists. At minimum it is recommended that standard data collection for all management fires include rate of spread, fuel weight consumed, and flame length. These factors must then be correlated to the effects of interest as well as the conditions which produced them.

A recent poll of research scientists and land managers has helped to identify future fire-related research needs (Kickert and others 1976). While these priorities, which are lumped into 24 problem areas, were identified for the coniferous forest type, they are applicable for most fire-type communities. Top priorities include the need for better information on the effects of fire frequency and intensity on succession, litter accumulation, and nutrient cycling.

Potential Conflict

One of the most important responsibilities of fire managers is to fully understand potential conflicts between their management actions and other resource values. Before a burning plan is approved, an evaluation of potential adverse as well as beneficial impacts should be made. Such impacts might include the effects of the fire on visitor enjoyment and use patterns. For example, it may prove desirable to temporarily close certain areas to public use because of potential danger or the obscuring of vistas by smoke.

While smoke from wildland fires is often considered as equivalent to other sources of air pollution, it does not contain significant levels of sulfur oxides, nitrogen oxides, or other common environmental pollutants (Hall 1972). What wood smoke does contain are large amounts of hydrocarbons and particulates. These are produced primarily through incomplete combustion and can cause temporary visibility problems.

For this reason it is often advisable that burning be conducted when wind will carry smoke away from populated or heavy visitor use areas. Smoke can also be minimized by burning at temperatures hot enough that near complete combustion occurs. Finally, while smoke produced in management fires may be temporarily disturbing it must be remembered that in the long run it is considerably less than that which would eventually result from a wildfire. At this point we can only hope that interpretations of the Clean Air Act will remain flexible enough to allow for prescribed and natural burn programs.

While to date most local air pollution agencies have shown a willingness to accept and work with fire management programs it is important that land managers make every effort to minimize potential problems. As an example of what can happen, a recent lightning-ignited fire in the natural fire zone of Rocky Mountain National Park jumped from a smoldering spot fire to over 400 ha in a couple of days. Local residents complained that business was being hurt by smoke and, as a result, Boulder County is considering a lawsuit against the Park Service for not having obtained a burning permit. Such instances emphasize the need to keep the public as well as surrounding agencies informed of and involved with an area's fire management program. We hope that when all alternatives are considered there will be little question but that perpetuation of "natural" processes is ultimately the best way to preserve natural ecosystems.

Other potential conflicts of which fire managers must be aware include the need to protect archeologic and historic resources and threatened and endangered species. The constraints recent legislation has imposed in mandating protection of these resources will require thorough inventories of potential burn areas. In addition, research studies are needed to determine the impacts of varying fire frequency and intensity on such resources. For example, it may turn out that certain endangered plant species are fire adapted and may be rare only because fire has recently been excluded from their natural habitats. In other cases frequent or intense fire may actually threaten the survival of a species. Experimental studies to determine the impact of fire of varying intensity on archeologic remains are currently underway in several National Parks (R. Kelly, personal communication).

Implementation

The success of a fire management program depends to a large extent on the interests and qualifications of persons charged with its implementation. Yet Moore (1974) has commented that in many regards "fire management concepts are ahead of personnel capability." Resource management specialists, fire control officers, and high-level management personnel must be professionally, technically, and attitudinally prepared before an effective integrated fire management program can succeed. Training programs should be designed to teach the basics of fire ecology and the artistic skills and scientific techniques of fire management. Field workshops and demonstration sessions should be effectively planned to share practical field experience as well as technical knowledge (Kilgore 1976). It would be especially effective if land management agencies and universities would jointly develop training programs, both for agency personnel and students, which would teach the appreciation of fire both as a natural process and as a management tool. An example of this type of training is the advanced Fire Management course given at Marana, Ariz., in past years.

Another area of concern involves the need to maintain close communication between researchers and managers. If fire managers are to benefit fully from available research findings it is essential that a two-way exchange of ideas and needs be maintained. If researchers are going to focus their attention on questions most vital to implementing prescribed and natural fire programs, managers will have to clearly articulate their needs. In addition, if fire managers are to fully benefit from available research, findings and conclusions will have to be communicated in a way that will be understandable to those without scientific training.

While it would be nice if all managers were also competent scientists, this is not and probably never will be the case. Thus, the current situation where research findings are communicated in technical reports is not sufficient. It is important that there be direct participation by both manager and scientist in evaluating application of research findings to everyday management problems. Participation by both managers and scientists in identifying important study topics and transferring findings into management programs is essential. The Forest Service has taken steps in recent years to facilitate both such needs (Kickert and others 1976, Mutch 1977, Lotan 1979). In addition, FIREBASE, a computerized bibliographic information file of fire-related documents is now available for users worldwide (Taylor 1977).

A final important step in implementing a fire management plan is the establishment of an effective public relations and involvement program (Kilgore 1976). Following decades of indoctrination that all fires are "bad," we are faced with the need to get across the "new" concept of fire management. As well as getting the public involved in future land management decisions, continued public relations efforts are needed to provide a full explanation of and justification for the need to use fire as a tool in maintaining natural ecosystems. In many cases what is needed is an increased educational effort directed toward understanding the natural role of fire in the environment, including what would happen should fire continue to be excluded (Stankey 1976).

CONCLUSIONS

If examples of naturally functioning ecosystems are to be preserved, it is obvious that fire will have to be allowed to play its natural role. This can be accomplished either through allowing naturally ignited fires to burn or, where fuel accumulations are so great as to threaten natural or cultural resources, by intentionally setting prescribed burns. This concept of using fire to achieve approved land management objectives is now referred to as "fire management." While the maintenance of effective suppression and control capabilities remains an important part of such programs, they do represent a considerable departure from the complete fire suppression policy which has long been in effect throughout most of the world. Such a shift in emphasis requires both retraining of experienced fire suppression personnel and reeducation of the public regarding the commonly held view of fire as an evil force (Vogl 1973).

While sufficient scientific information is now available to justify as well as implement fire management programs in many areas, there remain numerous research needs yet to be met. While many of these have already been mentioned, it is worth reemphasizing the lack of basic information on the natural role of fire in many of the world's native vegetation types. Perhaps the ultimate goal of areas developing fire management programs should be the ability to predict the short- and long-term consequences (on vegetation, wildlife, air quality, etc.) of any management fire (Lotan 1979).

Unfortunately, even the best applied research is of little value if it is not effectively communicated to and implemented by the concerned land manager. It is thus essential that close two-way interaction between research and management personnel be established. It is also important that managers accept and become personally committed to the role fire should play in the management of natural areas. The lack of such commitment has been blamed as one of the major reasons why more progress has not been made in the application of existing fire ecology knowledge (Kilgore 1976). As expected, it has been in those areas where managers have become personally involved that the most progress has been made in implementing progressive fire management programs (Daniels 1974, Kilgore 1975).

While the discussion in this paper has focused primarily on programs and needs on National Park Service and USDA Forest Service lands, the needs are the same and in some cases even more important on other public and private lands as well as in other parts of the world. It is especially important that the level of applied fire research

in other parts of the world be accelerated. For not only have most countries failed to implement integrated fire management programs, they have yet to recognize the need for fire in the preservation of natural communities (Parsons 1977, Lotan 1979).

In summary, the recognition and acceptance of fire as a natural environmental process is a necessary prerequisite to effective preservation of natural communities throughout the world. In those National Parks, Wilderness Areas, or nature preserves where naturally ignited fires cannot safely be allowed to burn, prescribed burning may be used to simulate natural processes. In either case, fire remains one of the most effective tools available for assuring the continuation of naturally functioning ecosystems.

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THE ROLE OF FIRE MANAGEMENT IN ALTERING ECOSYSTEMS

William A. Niering

Professor of Botany
Connecticut College
New London, Conn.

ABSTRACT

Prescribed burning is extensively used in wildlife, forest, and range management, and in maintaining biotic diversity. Burning tends to increase food and/or favorable habitat conditions for many upland game and waterfowl species. Prescribed burning in forest management is used in site preparation, removal of competitive species, and fire hazard reduction. Fire is used in preserving biotic diversity in natural areas by stimulating natural fire frequencies and intensities. Favorable forage species are also maintained by integrated fire management regimes. In altering habitats with fire, a holistic view must be maintained to preserve ecosystem integrity.

KEYWORDS: fire management, prescribed burning, forest, range, wildlife, natural areas.

INTRODUCTION

Fire was an important ecological factor in modifying natural ecosystems prior to the advent of European man (Kozlowski and Ahlgren 1974). Since lightning strikes the earth at an estimated rate of 100 times per second, there has been ample opportunity historically for lightning initiated fires to burn those vegetation types capable of carrying fire. Evidence of ancient fires comes from charcoal in deep ocean cores dated at over 10 million years, which is similar to charcoal resulting from forest burns on the Pacific coast. Fusain, fossil charcoal, has also been found in coal measures and resembles that from pine forests of Britain (Komarek 1976). Man's use of fire, a second source of ignition, goes back at least 500,000 years. In Australia, fire frequency increased with the advent of man, which has probably been true in most parts of the world (Cochrane 1968). In the northeastern United States, Day (1953) documents the role of Indian fires in modifying the oak-dominated forests of southern New England. The observations of Thomas Morton (1632) give some feeling of the frequency and intensity of Indian fires.

The Salvages are accustomed to set fire of the country in all places where they come; and to burn it, twize a yeare, vixe, at the Spring and at the fall of the leafe. . . . For when the fire is once kindled, it dilates and spreads itself against as with the winde; burning continually night and day, until a shower of raine falls to quench it. And this custome of firing the country is the means to make it passable, and by that meanes the trees growe here and there as in our parks: and makes the country very beautifull, and commodius."

It is also of interest to classify ecosystems based on their fire susceptibility or dependence. Vogl (1977) has categorized ecosystems as fire independent, fire initiated, and fire dependent. Fire-independent systems are normally free of fire during their development except under unusual circumstances where severe droughtiness or man's activities favor fire. These systems may include such areas as the wet tropics, desert, alpine fieldmark, and certain mesic temperate forests and wetlands. When fires occur in these systems they may be damaging since many of the taxa exhibit few adaptations to fire.

Fire-initiated systems are considered those vegetation types that may burn infrequently, but when fires occur they may be catastrophic. Such fires often occur on such long time scales that they are difficult to fully comprehend in terms of man's short lifespan (Wright, H. E., 1974). North American forest types such as eastern and western white pine (Pinus strobus, P. monticola), red pine (Pinus resinosa) as well as eastern and western hemlock (Tsuga canadensis, T. heterophylla), and western red-cedar (Thuja plicata), may fall into this category. In Australia, even the fire-sensitive mountain ash (Eucalyptus regnans), at the mesic end of the spectrum, appears to be this type (Mount 1969). Although they are all relatively long-lived trees, they have differential shade tolerances. Since the pines are more intolerant and the others more shade tolerant the trend within the pine forests is often toward more shade-tolerant species. With fire protection this often results in a physiognomic structure potentially capable of carrying a catastrophic fire, especially under droughty conditions. This increased fire susceptibility can also occur naturally in any of these types which is subjected to extensive blow-downs or insect damage which then increases the fire hazard. Such fire-prone conditions can also be favored by long periods of deliberate fire exclusion on the part of man. One might argue that the pines and E. regnans are actually fire-dependent types since they will not tend to be replaced without fire.

Fire-dependent or adapted ecosystems are of special interest to those concerned with ecosystem alteration since their perpetuation is highly dependent upon fire. In the temperate region, many grasslands and savannas and some deciduous forests including aspen (Populus spp.) and certain oak forests, as well as various pine forests such as lodgepole pine (Pinus contorta), pitch pine (Pinus rigida), longleaf pine (Pinus palustris), pond pine (Pinus serotina), and jack pine (Pinus banksiana) are fire-dependent types. In addition, many tropical and subtropical grasslands, savannas, and dry forest and eucalyptus forest types in Australia are fire types. Among the fire adaptations or requirements of fire-dependent species are (1) bare mineral or exposed substrate for seed germination, (2) removal of toxic or allelopathic chemicals or disease-causing conditions, (3) reproductive structures requiring fire to disperse propagules, and (4) ability to vegetatively reproduce by root suckering, stump sprouts, or epicormic stems. In addition, flowering or reproduction is controlled by fire in wire grass (Aristida stricta) and knobcone pine (Pinus attenuata) (Vogl 1968, 1974a, 1974b). Fire-dependent communities usually tend to accumulate heavy fuel loads and produce foliage that does not decompose rapidly due to its chemical composition or as a result of climatic conditions. This further accentuates the fire hazard. They are often even-aged stands dating from the last fire and are frequently dominated by shade-intolerant species or those of intermediate tolerance. Thus, fire-dependent

types may tend to develop toward more shade-tolerant stands, especially with fire protection. In some situations this protection merely increases the fire hazard conditions; in other situations a more mesic condition may develop which may minimize the chance of fire except during extremely droughty periods.

Traditional ecological succession and climax concepts have tended to place many of these fire-dependent vegetation types as "subclimax" types. If climax implies climatic control and fire is not considered a climatic phenomenon then this may be correct. However, to those who view fire as a natural ecological factor, these fire-dependent systems are really relatively stable "climaxes" under a burning regime, if historically it was a natural part of the environment. Such ecological recognition would give increased emphasis to the integral role of fire as a natural factor at a time when we are moving from a fire control to a fire management philosophy in our society (Kilgore 1976a, 1976b).

In fire management it is not only essential to understand natural vegetation trends (succession) with and without fire, but it is also important to understand the past role of fire in altering the present vegetation pattern one plans to manage. The structure of virgin forests of the Quetico-Superior Wilderness Area has been primarily controlled by natural fires (Heinselman 1973, Swain 1973). In this volume, Heinselman further documents the role of natural fires in this region. They are not old-aged stands, as often implied by the term "virgin," but have evolved with fire as a primary controlling force. It has also been documented that the present white and red pine stands in Itasca State Park, Minn., originated following major fires (Frissell 1973). In contrast, the apparent natural heath vegetation of Scotland is, in reality, a formerly forested area converted to shrub cover due to a long history of past burning and grazing (Kayll 1967). It should also be recognized that these anthropic types may now represent relatively stable types and that site conditions have been so altered that the so-called preexisting climax vegetation may not readily become reestablished even if fire is eliminated. For some time there has been a need to reevaluate our traditional Clementsian views of succession and climax as these terms apply to our interpretation of fire-influenced ecosystems. In this regard, it is timely and appropriate to cite the views of Egler (1954) in his study of the vegetation of arid southeast Oahu, where this meeting is being held. In this region which has been subjected to many introduced species and periodic fires he states:

Plant succession is deservedly one of the very creditable developments of students of American vegetation. In this study of Oahu, however, the writer prefers to use the term vegetation change, so as to embrace any and all kinds of temporal alterations within and between communities. The term Succession, in the minds of some, appears to denote a succession of step-like metamorphoses from one association to another. Furthermore, the retrogressive-progressive argument makes it necessary for one to know whether he is 'coming' or 'going,' a stand which the writer cannot always take for Oahu, and which others usually settle more by faith than by empirical knowledge. The climax, and God, have certain things in common for certain botanical atheists. To paraphrase Julian Huxley, the writer does not believe in the climax, because he thinks the idea has ceased to be a useful hypothesis."

It is critical not to burden the future fire literature with traditional terminology which, unless precisely defined, is often only clear in the writer's mind and may not be to the reader who has more progressive views concerning vegetation dynamics. The works of Egler (1954), Drury and Nisbet (1973), Wright and Heinselman (1973), Niering and Goodwin (1974), Vogl (1974b), and Connell and Slatyer (1977) emphasize the changing attitude.

Prescribed or controlled burning can be defined as the skillful application of fire to the fuel complex that will confine the fire to a designated area and produce an intensity of heat and rate of burn to accomplish certain planned objectives in wildlife, range, and silviculture management, as well as in other land uses. It may be used for a variety of purposes including: (1) removal of impalatable growth, (2) control of encroaching unwanted plants and certain diseases, (3) removal of fuel load to reduce fire hazard, and (4) creation or maintenance of favorable site conditions which in turn favor certain animal populations (Kayll 1974).

In this paper I shall explore some of the ways in which controlled burning has been or is being used commercially or experimentally to alter ecosystems and, secondly, attempt to demonstrate how scientific knowledge has played a role in guiding management practices.

WILDLIFE MANAGEMENT

In wildlife management, fire is now recognized as an ecologically sound technique in favoring certain game species (Miller 1963; Czuhai and Cushwa 1968; Komarek 1971; Vogl 1974a, 1974b); waterfowl, grouse, snipe, pheasant, bobwhite quail, turkey, woodcock, rabbits, hares, deer, elk, moose, black bear, beavers, and muskrats are among those populations which may be favored by fire (Vogl 1967, Kayll 1974, Lyon and others 1978). In contrast, species such as red squirrel, grizzly bear, marten, wolverine, fisher, and spruce grouse which are dependent upon relatively mature "climax" vegetation may be temporarily displaced by fire (Lyon and others 1978). In Africa, burning has also played an integral role in big-game management in the National Parks (Austen 1972, Brynard 1972, Owen 1972, van Wyk 1972, Joubert 1977).

Although the role of fire in wildlife management is often related to increased food production, there are also other factors involved. Fire often tends to create a mosaic of vegetation types or modifies the physiognomy of the vegetation by producing specific habitat niches critical to the survival of certain animal populations. Thus periodic fires maintain a heterogeneous vegetation pattern or a series of interspersions which tend to support specific wildlife species (Lyon and others 1978).

Game Birds

Stoddard's (1931) early use of fire in southeastern United States documented the beneficial role of controlled burning on bobwhite quail (Celinus virginianus) habitat. Opening of site conditions to favor food plants and feeding conditions for the young birds emphasized the importance of fully understanding the critical links in the life history of the species being managed. In Illinois, sharecropping (plowing and planting with grain) alone, or combined with burning also favors bobwhite (Ellis and others 1969). Thus favorable site conditions for the young may be achieved by agricultural activity in farming regions or by burning in forested areas, as in the South.

The ruffed grouse (Bonasa umbellus) is a wide-ranging woodland game bird favored by periodic habitat disturbance, a condition which may well have been created by natural fires in the past (Sharp 1971). Studies in Pennsylvania indicate that the three benefits resulting from fire are removal of heavy leaf litter, rejuvenation of food plants, and control of plant diseases. Spring burning reduced the leaf spot fungus on the slender stalk sedge (Carex debilis), a key grouse food plant. The interspersing of essential habitat components is also important (King 1938). Thus, interspersing spring burns every 2 years within grouse range is recommended, or a 4- to 5-year rotation when blueberries are also being favored. In the northeastern United States and Canada a 3-year burning cycle is typical for favoring commercial low-bush blueberry (Vaccinium spp.) production under "natural" conditions (Black 1963). Normal grouse population density is about one bird per 10 acres (4 ha), but under fire management one bird to 2 to 4 acres (0.08 to 1.60 ha) is optimal. Therefore,

Sharp (1971) concludes that the ruffed grouse is a fire "climax" species. Timber cutting also creates conditions favorable to grouse, but on a temporary basis compared to fire.

The prairie chicken (Tympanuchus cupido), whose habitat has been greatly reduced by prairie destruction, can be favored by burning. In Illinois, nest density 2 to 4 years after burning was one nest per 6 acres (2.4 ha) compared to one nest per 9.3 acres (3.7 ha) in unburned grassland. Along with the native prairie grasses, redbud (Agrostis alba) and timothy (Phleum pratense) can also provide suitable cover if burned in late summer (Westemeier 1973). In the Louisiana coastal prairies, the Attwater's prairie chicken (T. cupido attwateri), a nearly extinct species, is favored by burning or systematic grazing if frequency and intensity are controlled (Chamrad and Dodd 1973). They found that the bird's basic foods--seeds, insects, and vegetative shoots were all increased with burning compared to unburned ungrazed controls.

The sage grouse (Centrocercus urophasianus) is a western game bird of sagebrush grassland whose habitat has been greatly reduced by grazing and development (Klebenow 1973). Among the critical habitat factors are strutting grounds with low sparse sage or open denuded areas, nesting sites where total shrub cover ranges from 10 to 20 percent, and open grassy meadows as feeding grounds. In Nevada, preliminary burning in the spring appears to favor the habitat needs of these birds and creates a mosaic of cover types apparently present in the past when natural fires were more common. In many areas cattle grazing has so reduced grass cover that fires can no longer burn. Where there is an adequate fuel load, controlled burning provides a flexible and less expensive technique than herbicides (Klebenow 1973).

In the Pacific coastal region, fire had no significant effect on blue grouse (Dendragapus obscurus) over and above that of clearcut logging. Therefore, current clearcutting practices appear adequate in creating habitat openings to favor this species (Redfield and others 1971).

In Scotland, common heather (Culluna vulgaris) has been burned for some three centuries to maintain its productivity as forage for hill sheep and red grouse (Lagopus lagopus scoticus), a valued game species (Dep. of Agric. and Fisheries for Scotland 1977). The protein and ash content of the heather is highest in pioneer plants less than 7 years old (Gimingham 1971). Such data provide guidelines for establishing fire frequency since after 10 years the grazing value declines significantly. Therefore, burning at intervals not greatly exceeding 10 years is recommended to maintain maximum sheep and grouse production. Although these species are favored, data are limited concerning the effects of fire on other species (Miller and Watson 1974). Plants resprout vigorously following fire, but too frequent or intense fires diminish vigor and regenerative capacity to a point where other less desirable species such as bracken fern (Pteridium aquilinum) or deer grass (Scirpus caespitosus) become dominant. Density of grouse appears to correlate with food quality or amount of cover or both (Bendell 1974). The long-term effects of such burning on soil fertility, however, are still unresolved (Kayll 1967).

From these examples it is obvious that fire can play an important role in favoring a number of grouse species. Regional vegetation and climatic differences obviously modify the season and frequency of burning. In general, fire tends to create favorable site conditions which relate directly to the critical factors in the individual species' life history.

Big Game

The effect of burning on moose, elk, and deer has also been studied in terms of habitat needs and fire prescription. Spencer and Hakala (1964) indicate that moose management is concerned with early plant successional stages where deciduous browse

is available. In Idaho, spring burning increased aspen browse from a few hundred root suckers per acre to more than 25,000 in the aspen-Douglas-fir (Pseudotsuga menziesii) forest (Gordon 1976). In Minnesota, moose move from low growth aspen to mature aspen and willow (Salix spp.) in late winter (Phillips and others 1973). Thus maintenance of a mosaic of aspen size classes by burning at different times is desirable. Burning serves as an excellent technique in stimulating root suckering. In Alaska, response of moose to wildfires is not clear (Bendell 1974). Their populations did not always peak where browse conditions were most favorable (Spencer and Hakala 1964); however, they did following a 1947 fire when spruce (Picea spp.) was the major pioneer species (Lutz 1956). Although favorable habitats are created by burning, population response may not always occur in some parts of the range.

In northern Idaho, elk (Cervus canadensis) population density also appears to be closely correlated with wildfire. Early explorers reported few elk or deer in the Lochsa River drainage. However, after a major wildfire in the river system, the elk population reached peak density and then declined. Recent controlled burning in this drainage has dramatically lowered the browse line of serviceberry (Amelanchier alnifolia), willow, and mountain maple (Acer glabrum) (Leege 1968). The first year after burning all browse was below 7 ft (2.10 m) in height and even the second year 95 percent of the browse was still available, whereas on unburned plots only 28 percent was available. Thousands of acres of National Forest lands are now being burned to favor elk habitat. Another important winter range food especially favored by fire is redstem (Ceanothus sanguineus). Seedling establishment is dependent upon seed storage and fire intensity--the hotter the fire (optimum 212° F [100° C])--the higher the germination rate (Orme and Leege 1976). This further emphasizes the need to understand the life history of the species being favored and the fire intensity required to achieve one's objective.

Deer populations can also be favored by fire. Yet Bendell's (1974) synthesis of numerous papers results in no clear pattern as to the role of fire in the case of mule or black-tailed deer (Odocoileus hemionus). However, in California chaparral the amount of increased browse following fire is impressive. Decadent brush fields produce only 50 lb (20 kg) per acre with a 1 percent protein content, whereas following burning 2,000 lb (800 kg) of woody browse are produced with a 6 percent protein content (Hendricks 1968). In heavily wooded northern Wisconsin, spring burning was employed to perpetuate aspen, an important browse species for white-tailed deer (Odocoileus virginianus) (Vogl 1967). Deer use was higher on burned than unburned areas. Where fire is intense enough to stem-kill existing trees, white-tailed deer can have a dramatic impact in modifying habitat diversity by concentrating on resurging woody growth and so arresting tree and shrub development that a grassland is created. Such an incident occurred in eastern Pennsylvania where a 10- to 20-acre (4- to 8-ha) grassland was created by interaction of deer and fire (George Niering, personal communication). Within this oak forest region the area was still in grass 10 years after the fire. This may be one way in which grassy glades, widely reported throughout the Northeast, were created historically (Edward Komarek, personal communication). Subsequent fires would also serve to favor such grassy islands persisting within the forest matrix. Where agricultural activity is occurring, favorable habitat is perpetuated, thus keeping deer population high. However, in heavily or continuously forested areas periodic burning will create deer browse and help to maintain the population.

Africa also depends heavily on use of controlled fires to favor big game (Phillips 1965, 1974; Austen 1972; Joubert 1977). In Kruger National Park the policy adopted in 1954 states:

That until it is proved to be wrong, it be laid down by the Board as an interim policy that the whole of the Kruger National Park be divided into sections, separated by properly

constructed firebreaks, and that all grass which has become long and rank be burnt every three years on the understanding that only one third of each section be burnt annually and as late as possible in the spring after the first rains.

Although modified in more recent years, the general policy is sound and workable in favoring big-game species. In Kruger, withdrawal of fire from the veld and savanna woodlands leads to deterioration of grazing conditions and an increase in woody growth at the expense of graminoids (van Wyk 1972). Excessive burning can also lead to destruction of entire plant communities. The basic ecological premise evident here is that grassland should be either grazed, burned, or mowed to maintain its maximum vigor. In Malawi, Lemon (1968) found that burned grasslands were a strong attractant to wildlife after a few days, and served as a mechanism to keep animals from dispersing during the dry season when they might be more subject to various kinds of mortality, including poaching.

Fur Bearers and Waterfowl

Nearly two decades ago Givens (1962) indicated that fire was an accepted part of marsh management in our coastal wildlife refuges from Blackwater in Maryland to Sabine in Louisiana. Burning contributes directly or indirectly in providing adequate food for large populations of wintering waterfowl. Of 4 million acres (1 600 000 ha) of coastal marshes from Mississippi to Texas, it is estimated that 750,000 to 1,000,000 acres (300 000 to 400 000 ha) are burned annually. Although some are burned for livestock grazing, much is related to habitat improvement for fur-bearers, primarily muskrats, and waterfowl, especially blue geese (Perkins 1968). O'Neal (1949) recommends burning three-cornered grass marsh (Scirpus spp.) from October to January with a 0- to 2-inch (0- to 5-cm) water level. He states, "...without annual burns neither normal or peak rat populations can be reached." Sedge food plants are favored by fire over salt meadow cordgrass (Spartina patens). Pintails and snow and blue geese are attracted, but not Canada geese, since they are grazers rather than grubbers of roots and tubers (Hoffpauer 1968). The effect of burning on detritus production due to conversion of Spartina marsh to Scirpus would be of interest in terms of estuarine productivity.

In the Delta marsh of south-central Manitoba, spring burning of reed (Phragmites australis) prior to waterfowl nesting increases the marsh edge with a corresponding increase in nesting sites (Ward 1968). Ward feels that without burning, this marsh will cease to serve as waterfowl nesting sites and within a short time cease to exist altogether.

FOREST MANAGEMENT

In forest management in various parts of the world, prescribed burning is used in site preparation, removal of competitive species, or fire hazard reduction (Lotti 1962, Hodgson 1967, Liacos 1974, Trabaud 1974, Viro 1974, Martin and Dell 1978). In the United States, the largest prescribed burned area is in the southeastern evergreen forest region, especially on the coastal plain and Piedmont where over 2 million acres (800 000 ha) are burned annually (Cooper, R. W., 1971; Mobley 1972). Here, longleaf loblolly (Pinus taeda), and slash pine (Pinus elliottii) are among the more important forest trees being favored by fire. Longleaf pine has been most extensively studied with over 1,300 papers (Komarek 1974). In the absence of fire the successional trend is often from pine to hardwoods, such as oaks (Quercus spp.), hickory (Carya spp.), and sweetgum (Liquidambar styraciflua). Fire has also been found to be most effective in exposing mineral soil, especially conducive to pine seedling establishment. In the loblolly pine belt on the Piedmont it has been shown that twice as many seeds are required to establish seedlings on unburned compared to burned sites (Cooper, R. W., 1971). Fire is also used in conjunction with mechanical site preparation prior

to planting and then thereafter in fire hazard reduction and in arresting competitive woody growth. Research has documented that summer fires are most effective in killing or arresting hardwood competition up to 3 inches (7.5 cm) d.b.h. and simultaneously favoring wildlife habitat and cattle grazing (Lotti 1962). Herbaceous cover may be ten times more abundant and legumes five times more abundant on burned vs non-burned plots. In the absence of fire, herb cover tends to decline in 6 to 8 years. Another positive aspect that burning research has documented is the control of brown spot disease (Scirrhia acicola), a fungal infection of longleaf pine seedlings. Here winter burns are used at 3-year intervals until the pine seedlings are 6 ft (1.8 m) in height. Pedological studies indicate that prescribed burning on coastal plain soils does not decrease soil productivity except on highly erosive sites (Lotti 1962, Stone 1971). At this time all evidence suggests that fire is the most economical, least damaging technique in favoring pine and also serving as a technique in fire hazard reduction.

In the Great Lakes region, jack pine, and farther west, lodgepole pine represent two species with serotinous cones. In jack pine, the resinous bonds melt at 131° F (50° C) and in lodgepole at 113° to 131° F (45° to 50° C), where fire appears to be a selection agent (Lottan 1976). With such reproduction characteristics it might be argued that these forest trees are fire dependent and ecologically structured to periodically burn (Mutch 1970). Along with lodgepole pine, ponderosa pine (Pinus ponderosa) is another wide-ranging western mountain species whose fire history has been well documented (Cooper 1960, Weaver 1964, Biswell 1973, Biswell and others 1973, Wright 1978). Since fire has played an integral role in its evolution, fire protection over vast areas of its range has led to high fire hazard conditions. Historically, lightning-caused fires occurred at intervals of 6 to 7 years. They thus maintained low fuel levels, reduced competing vegetation, prepared seedbed conditions, and thinned seedling regeneration to prevent stagnated "doghaired" undergrowth thickets of pine reproduction. Controlled burning at intervals of 6 to 7 years, similar to the natural fire cycle in the past, has been shown to achieve these objectives in the Fort Apache Indian Reservation, Arizona (Biswell and others 1973). The effects and implications of fire management on various "climax" and seral ponderosa pine stands are presented by Wright (1978) in a recent state-of-the-art review. Once the potential catastrophic wildfire hazard has been reduced, a supervised burning policy for natural fires should decrease the potential of destructive fires.

In the Santa Catalina Mountains of Arizona decades of fire protection have resulted in many ponderosa pine stands with a dense undergrowth of pine. In the 1960's while studying vegetation of the range with R. H. Whittaker, we observed that there was a natural fire scrub vegetation locally within the ponderosa pine belt, mostly on rocky thin-soiled sites. However, an inventory of pine stands burned within the past few decades revealed that those burned by lightning-caused fires, which occur at a relatively high frequency in the range, were primarily open and parklike and dominated by muhly grass (Muhlenbergia montana). However, following a major man-caused fire, the intensity was so severe as to result in the complete destruction of an extensive pine stand, and the development of a fire scrub was favored which currently exhibits little or no pine regeneration. As is true in the establishment of many forest trees, open site conditions are essential, involving initial rather than relay vegetation floristics (Egler 1954). This implies that once the site is densely occupied by other competitive woody species, such as the dense oak scrub in this situation, tree reproduction seldom has a chance. Thus, with severe wildfires potential pine sites can be converted to oak scrub which may then persist since scrub is favored by repeated fires. The natural presence of fire scrub suggests that fires occurred historically, but creation of such extensive areas on more favorable sites suggests that accidental fires of such severe intensity were not common on such sites in the past.

The need for fire hazard reduction due to accumulated slash is a major problem in many forest types. Slash accumulation may reach 100 tons (90 t) per acre in Douglas-fir forests of the Pacific Northwest (Wilson and Dell 1971). Opening a mature mixed conifer forest can increase the fire spread by 4.5 times (Wilson and Dell 1971). In this region a single broadcast burn, often in the fall after the first rains, is usually adequate to remove the slash prior to seeding or planting (Dell and Green 1968, Dell 1976). In the National Forests, timber harvest by clearcut patches results in some 60,000 acres (24 000 ha) of slash which must be managed annually. In other forest types such as Virginia pine (*Pinus virginiana*), jack pine, ponderosa pine, and redwood (*Sequoia sempervirens*), prescribed burning is employed for slash removal and to prepare site conditions for seedling establishment (Ahlgren 1970, Little 1974, Weaver 1974).

Prescribed burning is widely used for fuel reduction in Australia where many of the 600 species of eucalypts (*Eucalyptus* spp.) have developed physiological adaptations to cope with fire (McArthur 1968, Crane 1972, Gill 1975). The evolution of vascular plant's adaptative traits to fire is reviewed by Gill elsewhere in this volume. The most extensive burning operations ignited by aircraft for fire-hazard reduction have been in western Australia. In 1965 three large areas totaling 53,000 acres (21 200 ha) were burned in 6 flying days (Baxter and others 1966), by dropping of incendiaries (4 g KMnO_4 and three safety fuses primed by ethylene glycol). Following priming in the aircraft, an exothermic oxidation reaction causes the mixture to boil and burning glycol ignites the fuses and plastic container on the ground. By dropping these incendiaries from the aircraft at appropriate intervals on a grid pattern there resulted a better than 8 percent ignition of spot fires. A total of 25,000 acres (10 000 ha) was burned within the 53,000 acres. With better conditions, a larger acreage could have been burned. In larger remote areas with few roads and no development this approach is feasible to accomplish fire-hazard reduction. Cost of ignition from aircraft was about 2.5 to 3.5 cents per acre. Two burns are recommended--one in spring and another in the fall. Cochrane (1968) cautions against too frequent use of fire in favoring introduced exotics or native species. In Victoria, the goal is to burn 750,000 acres (300 000 ha) annually and if fuel is kept at 1 to 6 tons (0.9 to 5.4 t) per acre (0.40 ha) a 4-year cycle will minimize fire hazard (Hodgson 1967).

In summarizing the influence of basic science on fire management in forestry, one must consider it in an historical perspective. The devastating forest fires of the late 1800's in the north-central United States, in which hundreds of lives were lost, surely helped to set the stage for the fire protection policy which has persisted over half a century (Haines and Sando 1969). These major fires occurred during peak drought periods and with a high slash fuel load due to lumbering operations. Once the policy was established, it was difficult to objectively evaluate the views of such early mavericks as Inman Eldredge, Roland Harper, and H. H. Chapman. As early as 1846, Charles Lyell, an English geologist, while touring open longleaf pine forests in Alabama, was told by university professors that this physiognomic aspect was due to frequent fires (Harper 1962). In 1890, Eldredge, forest supervisor of Choctawhatchee National Forest, proposed controlled burning to reduce the fire hazard. In 1909, Chapman, from the Yale Forestry School, urged the use of fire in longleaf for seedbed preparation and fuel reduction. In 1911, Harper, a botanist, also proposed its use to reduce fire hazard. Two decades later, there was sufficient evidence to justify prescribed burning in longleaf. As the scientific literature has grown, documenting the positive aspects of fire management, based on natural fire frequencies (Hendrickson 1972), there has developed a more rational approach in the discrete use of fire as a forest management tool as emphasized by the fire programs of the Forest and Park Services and fire management policies that have been revised. For example, DESCON (Designated Control Burn System) was approved in 1973 for the Francis Marion National Forest in the southeastern portion of the United States. DESCON allows either lightning or man-caused fires to burn under supervision when they meet preestablished fire prescription standards (Habeck and Mutch 1973, Loope and Gruell 1973, Devet 1976). Since then, policy changes have become more general.

MAINTENANCE OF NATURAL AREAS AND BIOTIC DIVERSITY

In the past few decades a large number of natural areas--living museums--have been set aside by such agencies as the USDA Forest Service, The Nature Conservancy, and The National Audubon Society. This is an effort to preserve elements of our natural heritage which are rapidly disappearing with continuous development and urbanization. Initially, it was felt that total protection from any manipulation by man seemed desirable, but as sound ecological data have become available, more realistic schemes have evolved in which controlled burning is now part of certain management plans (Boardman 1967, Gill 1977).

The Konza Prairie Natural Area, a 916-acre (366.4-ha) tract in Kansas, acquired by The Conservancy in 1971, is now under a fire management regime in which six treatments have been established involving 1-, 2-, 4-, and 10-year burning intervals. In addition, areas will be burned after years when precipitation reaches at least 1.2 times the median. It is anticipated that these various fire frequencies will encompass the range of fire occurrence previous to settlement by European man (Hulbert 1972) and therefore serve to alter and eventually restore natural fire conditions and the floristic richness typical with past fires.

At the University of Wisconsin, the planted Curtis Prairie, created by the late Dr. John Curtis, was initially burned in the spring of 1950 and has since been fired on a 2-year cycle (Cottam and Wilson 1966, Anderson 1973). The ecological basis for this plan was founded on field research of Curtis (1950) and Curtis and Partch (1948). Controlled fires are also being used in Wisconsin's scientific prairie areas to arrest woody invasion and maintain prairie conditions (Vogl 1967).

The National Parks also represent living museums where prescribed burning is being used to restore natural conditions. In the late 1950's, fire was used in Everglades National Park to favor pine over hardwoods. Since then hundreds of burns in various vegetation types have occurred and now natural fires and certain man-set fires are being allowed to burn (Parsons 1976, 1977). The role of fire management in maintaining natural ecosystems is covered by Parsons in this volume. In the West, Kilgore (1972, 1975) has pioneered the use of fire in Sequoia and Kings Canyon National Parks to alter the course of vegetation development. Without fire, white fir (Abies concolor), was appearing under the giant sequoias (Sequoiadendron giganteum). Tree ring studies have shown that a minimum fire frequency of 7 to 9 years occurred prior to European influence (Kilgore 1973). Such data have served as a guide in the fire management program. From 1968 to 1978, prescribed burning was extended to twelve National Parks and Monuments where it is aiding in the preservation of landscape diversity. In Lebanon State Park, N.J., prescribed burning is used on recreation areas for improving visibility, increasing wildlife, and reducing the fire hazard. Undergrowth vegetation is also rejuvenated. In addition, fire acts as a sterilizing agent on tarspot (Rhytisma andromedae) on mountain laurel (Kalmia latifolia) and promotes increased flowering and fruiting of ground cover species (Cumming 1969).

In the Black Mountain Reserve, a natural preserve in Canberra, Australia, a set of fire plots was analyzed by Dr. Rosemary Purdie and the author several years after prescribed burning in a dry sclerophyll forest (Eucalyptus macrorhyncha and E. rossii). Here, shrub cover was dramatically increased on certain plots either from seedling origin or sprouting. In addition, species diversity among shrubs and herbs was dramatically increased. This included several species of orchids. In general, shrub cover was especially favored by fire in contrast to other forest regions where woody undergrowth is usually suppressed. The pre- and postburning vegetation pattern was more conditioned by site or exposure than by fire intensity. Use by kangaroos was also observed during the study, especially in the more grassy mesic sites.

In the southeastern evergreen forests of the United States, controlled fires have also been reported to favor certain wildflowers, including pitcher plants and several species of wild orchids (Komarek 1965, 1974). We may find with further research that the preservation of certain of our rare and endangered species, including endemics, may be favored by prescribed burning. However, in England, Moore (1976) reports some devastating effects of wildfires in the heathlands on two rare reptiles in the Hartland Moor National Nature Reserve. An original population of 800 sand lizards has been reduced to 30. Possibly controlled burning in small strips or patches would have prevented this catastrophe.

Maintenance of favorable breeding habitat for the Kirtland's warbler is a unique example of habitat alteration to preserve a rare species of songbird. In the Huron National Forest, Mich., habitat requirements of this species are being favored by cutting, burning, and planting in order to provide dense jack pine stands from 5 to 15 ft (1.5 to 4.5 m) in height interspersed with small openings (Miller 1963, Buckman 1964, Cayford 1971). It is only in this specific physiognomic vegetation structure that the Kirtland's warbler completes its life history. In Arizona, Marshall (1963) also reports that bird diversity is correlated with preferred habitat requirements, primarily grassy openings favored by fire.

Prescribed Burning in Southern New England

In the Connecticut Arboretum at Connecticut College, we are attempting to maintain maximum habitat diversity by the creation of two natural areas and manipulation of other landscapes with herbicides and fire. In 1968, controlled spring (March and April) burning was initiated in postagricultural oak-dominated forests and abandoned pastures with well-drained sandy loam soils. In nearby Pachaug State Forest, an oak-pine forest and a 40-year-old red pine plantation were also burned. Since fire was important during the Indian period, we were interested in re-creating, if possible, open parklike forests typical of that period (Morton 1632). We were also interested in the effects of fire on floristic composition in forests and fields and especially on the productivity of little bluestem (Andropogon scoparius) grassland. In biennial forest burns, highest tree mortality occurred among oak, black birch (Betula lenta), and black cherry (Prunus serotina), less than 6 inches (15 cm) d.b.h. (Niering and others 1970). Where cambial temperatures reached 212° to 392° F (100° to 200° C) for 2 to 7 minutes, hickory and black birch 2 inches (5 cm) d.b.h. were completely root-killed, whereas white pine subjected to normally lethal 140° F (60° C) survived. The thin-barked birch exhibited the greatest mortality in all size classes and has been essentially eliminated from burn plots. Larger black oak (Quercus velutina) and beech (Fagus grandifolia) 10 to 13 inches (25 to 32.5 cm) d.b.h. survived external temperatures to 129° F (54° C) for 7 and 11 minutes, respectively, although basal scarring of beech occurred. With removal of the cherry understory only scattered cherry sprouts persist in the shrub layer. Herbaceous cover, especially grasses and sedges, now forms the dominant ground cover (5 to 10 percent) in addition to spotted wintergreen (Chimaphila maculata) which is favored by burning. Tree and shrub seedling reproduction increased 12-fold over controls and floristic diversity increased 50 percent compared to unburned plots. Burning created an open parklike forest somewhat similar to that reported during the Indian period (Morton 1632). Trees over 6 inches (15 cm) d.b.h. are vigorous except for occasional fire scars which occurred primarily during the initial burn. This burning regime has resulted in fire hazard reduction, increased floristic diversity, and the creation of an esthetically interesting forest. Fire scarring of larger trees could be avoided by removal or wetting of heavy litter accumulation around the bases of trees prior to the initial burn.

Annual and biennial old-field burning has favored little bluestem; standing crop biomass (average 136 g/m²) increased 20 percent compared to a comparable decline in unburned

controls (average 247 g/m²). Floristic stalk production increased 24 percent in burned vs. unburned areas. Two conspicuous fire increasers were the forb wild indigo (Baptisia tinctoria) and the shrub sweetfern (Comptonia peregrina), both nitrogen fixers. In fact, little bluestem and rough goldenrod (Solidago rugosa) reached their maximum vigor in association with sweetfern. Huckleberry (Gaylussacia baccata), winged and smooth sumac (Rhus copallina, R. glabra), aspen, bayberry (Myrica pensylvanica), wild rose (Rosa spp.), arrowwood (Viburnum recognatum), greenbrier (Smilax rotundifolia), oaks, and black cherry are fire persisters and resurge following old-field burning. A greenbrier thicket was converted to grassland by heavy rabbit browse on the succulent resurge following the first few burns. Goldenrod, as well as woody growth already established, tends to increase in unburned grassland plots. Flash fire temperatures reached 1,004° F (540° C) but Tempilaq-marked bars only reached 221° F (105° C). Biennial burning is recommended to maintain a highly productive little bluestem grassland. Annual burns may be too frequent on well-drained sites unless soil moisture is adequate. Such burning does not completely kill most associated woody growth, but rather stem kills and stimulates resurging of existing woody species. In fact, the clonal spread of sweetfern is markedly stimulated by annual burning. However, where little bluestem is dominant, it can be perpetuated by fire and add landscape diversity of high esthetic quality. Little bluestem grassland represents an element of prairie within a dominantly forested mosaic--a pattern which existed historically.

Burning the white pine-oak forest failed to result in white pine establishment even with a nearby seed source (Ahlgren and Ahlgren 1960). However, prescribed burning resulted in the selective perpetuation of all size classes of pine although many stems less than 6 ft (1.8 m) high were root-killed. Based on these data, one might hypothesize that burns of low intensity in the past may have served to selectively favor white pine which is relatively sensitive to fire, especially when young.

The initial burn in the red pine plantation reached the most intense litter temperatures recorded--in excess of 644° F (340° C) (Tempilaq). Dominated by pine 9 to 12 inches (23 to 30 cm) d.b.h., none was killed except scattered smaller suppressed pine. The fire served to reduce undergrowth and stimulate browse--two objectives of the burning. It is also hypothesized that such fires may be an effective tool in arresting root rot (Fomes annosus) outbreaks which are currently taking a heavy toll in such stands in southern New England (Cooper, R. W., 1971).

This controlled burning research in the Connecticut Arboretum has served a multiple-purpose function. It has provided data on the effect of such fires on the floristics of forests and old-field communities; it has maintained or increased the landscape diversity within the Arboretum where the trend without fire is toward an increase in forest species. These readily accessible study plots also provide an invaluable set of demonstration areas where students and the public can be introduced and educated to the role of fire in natural ecological systems.

RANGE MANAGEMENT

In the southern pine and ponderosa pine regions the burning regimes previously mentioned have multiple-use benefits including the production of suitable grazing land (Weaver 1968; Vogl 1973, 1974b). The current trend in range management is to promote and integrate the use and control of fire (Bourassa and Brackebusch 1978). Fire is also being used in the coastal prairies of Texas to reclaim some 80 million acres (32 million ha) of woody plant infested rangeland. Some 500,000 acres (200 000 ha) are infested with Macartney rose (Rosa bracteata), an introduced species which is now being controlled by an integrated vegetation management control system involving herbicides and/or winter burning. With adequate fuel and windspeed, stem-kill occurs and with periodic burning thereafter woody growth is suppressed (Gordon and Scifres 1977) and herbaceous cover is increased. Another technique involved the application of

herbicides followed by fire (Scifres 1977). Huisacke and white brush are two other species being controlled by fire along with mechanical techniques. In the coastal prairie region, Gulf cordgrass (Spartina spartinae), covering some 200 million acres, is also being subjected to experimental burning. Although unpalatable when mature, following burning it has a higher protein and phosphorous content than mature unburned grass (Oefinger and Scifres 1977). Fire is also used in mesquite (Prosopis glandulosa) and tobosa (Hilaria mutica) communities of west Texas to remove accumulated litter, increase grass palatability, reduce mesquite, and kill undesirable annual broomweed (Xanthocephalum dracunculoides) (Wright 1974). Burning should be done during the dormant season when the soil is relatively moist. In the Great Plains, cool season annuals are controlled by spring burning.

Much of this woody encroachment in Texas rangeland and that observed in the desert grassland farther west has been induced by overgrazing. Mesquite, another grazing increaser, was much less widespread prior to the introduction of cattle (Humphrey 1953, 1958, 1963, 1974). Although prescribed burning has been used to arrest mesquite, there has been limited success (Cable 1967) which is not unexpected since fire intensity would be greatly modified with grazing. Prior to the introduction of cattle, grass cover was sufficiently dense and capable of carrying frequent fires which would arrest small invading woody growth. Since overgrazing has greatly reduced the fuel load and sizable woody growth has developed, the degraded desert grassland fails to respond to fire as it did in the past (Sauer 1950, Humphrey 1953, Malin 1953).

Pasture or field burning has also been widely employed throughout the world for removing crop residues, for stimulating succulent new forage, and also for sanitation purposes (Komarek 1965, Hardison 1976). In southern and eastern England some 2.5 million tons (2.25 million t) of cereal crop residues are burned annually (Bullen 1974). Data suggest that, although a somewhat controversial practice from the older plowing-in technique and/or disposal, straw burning helps control certain weed problems. Burning grass seed fields in the Pacific Northwest for disease control was initiated three decades ago (Hardison 1976). However, recently this practice in the Willamette Valley has been challenged as lowering air quality. Mobile incinerators developed at Oregon State University show great promise in reducing particulate discharge (Bonlie and Hudson 1971).

Fire management has also been employed in clearing chaparral and converting it to pasture lands. In the Tonto National Forest, Ariz., aerial sprays of 2,4,5-T were used as a dessicant, followed by burning and then repeated herbicide spraying to further arrest woody development (Baldwin 1968). Mechanical removal is also practiced followed by fire and seeding. These are rather drastic land management techniques and one might question the ecological soundness of aerial applications of 2,4,5-T today. However, positive benefits in terms of increased water yield have also been reported following these treatments (Zwolinski and Ehrenreich 1968).

In the National Forests of California, chaparral is also being converted to grazing land. Removal of chamise is followed by seeding and several fires are required thereafter to arrest woody growth and favor grasses (Biswell 1963, 1974; Doman 1968). Although beef production on such converted chaparral land was increased fourfold (Raymond 1968), Biswell (1974) questions the desirability of reseeding burns on certain sites. Since chaparral is a fire type and becomes decadent after 40 years, fire-hazard reduction burning is recommended. In California, spring burns from March to early May appear best when vegetation is not too dry and strong winds are less frequent (Biswell 1974). Under this regime excellent wildlife and sheep browse is created and this vegetation type is perpetuated (Murphy 1968). However, with less rangeland being burned as land use patterns change, fire-hazard reduction may become the major use of prescribed burning and vegetation conversion for fire control (Westman 1976) in much of the California chaparral country.

CONCLUSIONS

Scientific knowledge has played a major role in the controlled use of fire in altering ecosystems. Fire frequency and intensity are key factors in achieving one's desired objectives whether toward favoring a specific species or more general goals that frequently result in multiple-use values. For fire hazard reduction, frequent light fires are usually desirable, whereas for stimulating seed germination or seedbed preparation for certain species, i.e., eucalypts, hot fires are essential.

In wildlife management, understanding the critical links in the life history of the species being favored is paramount. Most wildlife and game species are favored by vegetation disturbance which stimulates new woody and herbaceous growth either by sprouting, suckering, or seedling reproduction. Under natural conditions this can result from lightning-caused fires, severe storms, droughts, and insect epidemics. Under man's influence these conditions can occur as a result of fire, clearing, cutting, and agricultural activities. Although game species are often favored by prescribed burning, our knowledge is still incomplete in many sites concerning total ecosystem response, especially on nongame populations both in terms of short- and long-term responses (Lyon and others 1978). How is animal behavior modified by fire? Is favoring specific species, often for man's benefit, resulting in any long-range deterioration of the system under a specific burning regime?

In vegetation management it is basic to understand the historical role of fire as well as the patterns and processes of vegetation change which tend to occur with and without fire. In the restoration of natural fire regimes, prescribed burning techniques should attempt to simulate the natural fire cycle. Here, tree ring studies indicating past fire frequency can prove invaluable. In grasslands it should be recognized that the mere introduction of fire into a system seriously disturbed by man may not result in its restoration to pre-European man conditions. Here, integrated vegetation control systems involving chemical and/or mechanical treatments, along with fire, may be needed.

As ecosystem alteration using fire increases around the world, there should be an awareness of the role that biological diversity has played in the scheme of ecosystem evolution. Our efforts in the sound use of fire should consider the creation of "patterns that contain the unexpected" (Cooper, C. F., 1971) rather than the creation of vast acreages of homogeneity. As we tend to favor resources to fulfill man's needs we should not lose sight of the pattern fire played under natural conditions in creating a constantly changing mosaic of vegetation types.

When fire management is directed toward maximizing a specific resource, it is still essential to maintain a holistic view of ecosystem processes. One must be constantly on guard for nutrient leaks within the system. We know that man-manipulated systems can be very leaky compared to natural systems (Likens and others 1970, Woodwell 1978). As the cost of fossil fuel-powered management techniques increases there may be a shift to the use of energy efficient techniques. Although fossil fuel-powered equipment to arrest unwanted plant growth has become a way of life in the highly affluent countries of the world, there is increasing evidence that fire has the potential of serving as an alternative with high energy conservation values. It is employed in railroad right-of-way maintenance in Australia, and in the United States it has proven feasible on certain transmission rights-of-way in vegetation management in the South (Arner and others 1976).

As our industrial air pollutants are brought under control, the less harmful natural "pollutants" from controlled and supervised natural fires may prove to be tolerable, considering the overall benefits. As indicated by White (1972) "sensitive, wise management does call for a state of deepened knowledge and of genuine freedom from conventional modes of thought." Such will be reached "by candid innovative assessment of the whole range of possible adjustments, now, or as the fruits of research open

to man." However, in all our enthusiasm we must retain a holistic view and place fire in its proper perspective along with the complexity of other interacting factors which are operative in maintaining ecosystem stability and diversity. Fire must still be viewed as a servant, not a master, in our manipulation of natural and man-created landscapes.

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FIRE CYCLES AND MANAGEMENT ALTERNATIVES

J. Harry G. Smith, Ph.D.

Faculty of Forestry
University of British Columbia
Vancouver, B.C.

ABSTRACT

Information on age classes for British Columbia obtained in the 1957 inventory is used to show changes in species composition and effects of fire before and after settlement. Effects of wildfires, logging, and other disturbances on species composition are documented for four inventory periods, before 1831, 1831-70, 1871-1910, and 1911-50. Disturbance has favored Douglas-fir, lodgepole pine, and hardwoods at the expense of cedar, hemlock, and spruce. Species distribution by age class is also used to determine mean forest ages and lengths of fire cycles. Times required to replace forests by fire (fire cycles) are calculated for all major regions and species groups, assuming that occurrence of killing fires follows either the negative exponential or Weibull frequency distributions. Recent data on areas in forest types and areas burned by types and bioclimatic regions are used to show that fire cycles have been lengthened, probably as a result of intensifying forest protection. Average fire cycles now may be 10 times longer than those in presettlement forests and indicate an acceptable level of fire control. Limitations of methods and data employed are outlined and suggestions made for extension and refinement of analyses.

Data on mean ages, fire cycles, and areas disturbed establish effects of disturbance in natural forests followed by major changes during settlement and urbanization and then by gradually improving fire control. As fire control approaches general levels acceptable to sustained yield, timber managers' attention soon should be directed to careful analyses of fire damage and benefits in relation to costs, with full consideration of all resource and social values at risk. Major alternatives ranging from nearly complete fire exclusion to carefully planned fire use exist and should be evaluated fully by fire managers and resource managers.

KEYWORDS: negative exponential, Weibull frequency distributions, mean age class distributions, areas burned, fire effects, fire economics.

INTRODUCTION

Much new information about the effects of fires on ecosystem development has been obtained by studying age class structure for major regions and species groups of British Columbia (B.C.), Canada's most western Province. Data on fire frequency and areas burned by forest types gleaned from records of the Protection and Inventory Divisions of the B.C. Forest Service should be of interest to protection specialists and fire scientists responsible for similar forests in adjacent Pacific Northwest States and Alaska. Few quantitative data are available on fire intensity, but improving utilization and better fire control have, no doubt, reduced soil damage from fires in slash and old burns in recent decades.

Bases for decisionmaking, fire control standards, fire intensity, recent fire losses, and evidence of past fires are described. Effects of fire and other disturbances, changes in proportions of area by species groups, influences of species, site, and bioclimatic zone on average and stand plot ages, and fire cycles are illustrated with tables. Results of intensified fire control, influences of research, and options for modern fire managers are identified with special emphasis on B.C. Unless otherwise indicated, all data and information discussed apply to B.C.

BASES FOR IMPROVED DECISIONMAKING

Although there has been much interest in the logistics and biological aspects of fire control, there has been little consideration of economics. Research efforts of the Canadian Forestry Service in British Columbia have emphasized fire danger rating and sought to provide useful solutions to important operational problems (Kiil 1975) such as faced by the Protection Division of the B.C. Forest Service.

Forest fire weather zones in British Columbia range from minimal risk on the outer Coast to the Southwest Dry Belt and East Kootenay Regions in Southern B.C.--the most extreme in Canada (Simard 1973). Simard (1975) analyzed wildland fire occurrence in 1961-66. He found the highest fire occurrence (more than 20 fires annually per 1,000 mi²) (2 590 km²) along roads in southern B.C.

Improved decisionmaking by fire managers requires sound data on costs, production, and net percent losses (Simard 1976). Costs are determined by the effort devoted to fire management. To keep costs low, there should be a least-cost optimization of the mix of production factors. Better understanding of fixed and variable costs associated with fire control and impacts of fire damage on landowners, local users, and general public are needed to make fire management more efficient. While reducing fire occurrence, speeding fire control, and diminishing fuel hazards, fire managers should strive for an optimum mixture of production factors. The price of each factor divided by its marginal productivity should be equal to the comparable ratio for every other factor (Simard 1976). Damage should be evaluated at several levels. Objective data on net present value are needed to enhance economic efficiency, but estimates of replacement costs and of all gross values at risk should also be made to help fire managers compete with other politically alluring uses of public funds. Of course, net benefits should also be determined for the growing number of situations in which wildfires enhance rather than diminish habitat values. Although many potential gains from economic analysis of fire management options are conceded and potential research gains are admitted to be high, most fire control agencies have poor control of costs, few data on actual control times and rates of fireline construction, and often rely on rough schedules of damage to make their case for better funding. Nautiyal and Doan (1974) showed how studies of equal dissatisfaction of a forest owner might be useful in study of expenditures on forest fire control. They suggested that in some cases extra revenue from cutting more area than planned could be used to finance protection expenditures to reduce expected burning damage and, thereby, improve overall public satisfaction with reference to forest resources management.

A useful approach to evaluation of wildfire damage and benefits and methods for determining values of all resources protected has been developed by Crosby (1977). Brown and Boster (1978) illustrated the importance of evaluating how a fire and associated damage might change outputs of usable goods and services. The importance of stressing values saved from fire was advocated by Martell (1978). The need for a standard appraisal system on all Federal lands was illustrated by Noste and Davis (1975). Commendable progress in damage appraisal has been reported by the Canadian Committee on Forest Fire Control (1979).

FIRE CONTROL STANDARDS

Since Beall's 1949 pioneering study using area burned as a standard of forest fire control, there have been few improvements. His percentages of area burned each year still are the most widely used index of fire control's effectiveness. Kun's (1958) concept of targeting a reducing proportion of area burned as a basis for improvement has not been widely applied. Many other economic questions should be answered by careful analysis (Smith 1971).

Despite increasing concern for improved planning and tighter budgetary control, no major forest fire control agency has succeeded in using well-defined performance standards. This may have been partly because average fire seasons tend to be exceptions rather than rules (Simard 1975). Also, damage has been notoriously difficult to estimate and often is so undervalued that it seems as if the marginal dollar in cost of improved protection buys too few cents of marginal damage prevented. In 1976, with damage estimated at \$2.5 million and B.C. Forest Service expenditures 1975-76 on fire suppression costing \$8.3 million, spending additional dollars might save only 30 cents, if the objective is to minimize cost plus loss. Only if loss to the Provincial economy could be demonstrated as actually approaching the 10 times damage claimed could additional suppression dollars be justified as providing reduced damage benefits in relation to their costs. Most expenditures are supported by vague estimates of values at risk, worries about potential losses of jobs and lives, and concerns about what could happen in repetitions of disastrous years that have occurred too frequently in the past.

FIRE INTENSITY

There are no data on fire intensity, but in slash fires it has been substantially reduced by improved utilization as a result of the growing demand for wood. As smaller logs and more species are removed by logging, slash consumed by wildfires and slash-fires decreases greatly (Morris 1934). In the past 30 years volume utilized per unit area on the Coast has doubled (Smith 1978). In 1976 volumes harvested from Coastal forests averaged about three times typical Interior yields. Precommercial thinning on the Coast can lead to "explosive" hazards (Lawson 1979).

Combination of poor utilization and severe droughts 1890-1935 means that wildfires in slash during that period were much more intense than those in recent years. Similarly, wildfires that burn forests during severe droughts consume much of the forest floor (The World 1906).

In many Interior forests, removal of natural, periodic, sublethal fires by effective fire control and overgrazing (Parminter 1978) has enhanced potential fire intensity increased the chances of major fire damage, and resulted in severe insect damage (Wickman 1978).

EVIDENCE OF PAST FIRES

As methods of determining fire history improve (Arno 1976, Arno and Sneek 1977) and recognition of the natural role of forest fires grows, interest in documenting

location, timing, and intensity of past fires in British Columbia increases. Charcoal is present in most British Columbia soil profiles. Charcoal also has been found below the volcanic ash spewed out by Mount Mazama more than 6,600 years ago (Smith 1974). Early explorers and journalists described effects of many large wildfires in the 1800's (Morris 1934). Early silvicultural investigators employed evidence of the fire scars on Douglas-fir and ponderosa pine to determine fire frequency and document the need for improved fire control. For South Coast Douglas-fir, Leavitt (1915) reported that from 1895 to 1915 frequency of fires had increased enormously to one every 5 years. This was much greater than the intervals of 27 years for the previous century and 86 years for the period 100 to 360 years earlier near Powell River, B.C. For the Interior, the B.C. Forest Service observed in its 1923 annual report that 2 percent of the ponderosa pine in merchantable stands were badly fire scarred. Fire scars on one tree in the Kootenay District indicated 13 fires in 193 years, an average interval of 15 years between fires. For Interior Douglas-fir growing at the grassland edge on Dester Ridge west of Williams Lake, Parminter (1978) found evidence of 17 fires between 1759 and 1926, then no fires while protection improved to 1978. The interval between fires on the Ridge was about 10 years.

Years of stand establishment of Coastal Douglas-fir were determined by Eis (1962) as an indication of fire history. Schmidt (1970) observed that in presettlement days regeneration of Douglas-fir depended almost entirely upon the occurrence of forest fires when periods of extended drought coincided with intensive lightning storms. He observed that extensive major fires which occurred 150, 230, 310, 360, 410, 560, 760, and 870 years ago were well represented by Douglas-fir and there were fragments of older stands established between 940 and 1,300 years ago.

Tree-ring analyses (Smith 1970b) can determine years in which tree growth has been particularly slow because of drought. In the Interior, 1623 and 1869 were particularly dry years, and 1885-1925 was much drier than any period in the previous two and a half centuries.

Fire statistics published since the establishment of the B.C. Forest Service in 1912 have been analyzed to consider the future of prescribed burning (Smith 1970a), the impact of fire control on ecosystem development (Smith and Henderson 1971), the amount of protection needed (Smith 1971), and the use of fire in Canadian forests (Smith and Henderson 1972). Rates of spread and fire damage were related to areas in timber cover types for the forest districts and bioclimatic regions of B.C. (Smith and Gilbert 1976). Smith (1970b) and Smith and Henderson (1972) drew attention to the B.C. Forest Service inventory of age classes by zone and type group as a basis for illustrating impacts of past natural fires and recent development upon the forest.

HISTORICAL EFFECTS OF FIRE AND OTHERS DISTURBANCES

Early Fires, Logging, and Other Disturbances

Past fire damage has greatly exceeded disturbance by logging and all other factors. Whitford and Craig (1918) estimated that 665 billion bd.ft. (3.14 billion m^3) of timber had been destroyed by fire. This was 32 times the volume logged by 1918. They observed that timber on about 64 million acres (25.9 million ha), or two-thirds of the land once forested, had been "totally destroyed" by fire, and on over half of the area left timber was seriously damaged. Early logging took the remaining best stands and valley bottom types first. To compare logging with fire, note that the 341 billion bd.ft. (1.61 billion m^3) harvested to the end of 1976 was logged from roughly 10 million acres (4.05 million ha) (Smith and Kozak 1970, annual reports of the B.C. Forest Service 1912-76). Even with improved fire control, from 1912 to 1976 wildfires burned 23.2 million acres (9.39 million ha).

Approximate areas logged and burned since 1912 (table 1) appear large in relation to the 1.9 million acres (0.769 million ha) of improved farmland recorded by the 1976 census. A similar total area, 1.85 million acres (0.749 million ha), is in "organized" areas, but only 232 thousand acres (93.9 thousand ha) or 12.5 percent of that is in cities, towns, and villages (Smith 1976a). Logging and fires probably had already disturbed much of the land now in farms and urban areas.

Between 1913 and 1940, 294 thousand acres (119 thousand ha) of logging slash and 1.068 million acres (0.432 million ha) of clearing slash was burned under permit (Smith 1970a). Clearing was done for agriculture, railway rights-of-way, and public roads. Recently, large areas such as 420 thousand acres (170 thousand ha) of Lake Williston have been flooded for hydropower generation.

Although forest insect and disease data have been collected since 1937, damage is highly variable and net area killed has not been routinely determined. Impacts of insects, disease, and climatic extremes often have been severe, but it is still not possible to document actual timber areas lost annually (Harris 1976). Many outbreaks destroy species or size classes which are replaced in time by other trees without killing the whole stand.

Areas logged have been reported by the B.C. Forest Service only since 1971. Most logging harvests oldest stands first. No logging of immature stands has been allowed by the B.C. Forest Service. Under full utilization of productive forests, on a 100-year rotation, which is average for B.C., 1 percent of the area of weighted average sites should be harvested annually. This could amount to 1.2 million acres (486 thousand ha). The maximum area logged to date was 428 thousand acres (173 thousand ha) in 1973.

Following disturbance by fire or logging, natural regeneration can take place over a considerable period, which depends very much upon habitat type, nature and extent of disturbance, distance from seed sources, and timing of good seed years (Smith 1975). If disturbance is complete, regeneration delay may average 5 years on wet sites and 10 years on dry sites. Regeneration may continue over a 20-year period and in large burned areas may not become complete until pioneer trees reach seed-bearing age. If logging or other disturbances do not destroy the understory, released advance growth may combine with natural regeneration. The 1957 B.C. Forest Service inventory estimated that 44 percent of Coast forests and 14 percent of Interior forests possessed "satisfactory" understories, i.e., 200 or more potential crop trees per acre (494 per ha) of desirable species, in trees between established seedling size and 13.0 inches d.b.h. (33 cm). Acceptance of true firs as potential crop trees would have substantially improved the Interior situation.

TABLE 1.--Relative areas disturbed by wildfire and logging, 1912-76

Period	Approximate areas disturbed annually by		
	Wildfires (W) ^{1/}	Logging (L) ^{2/}	W/L
	- - - - -Thousands of acres- - - - -		
1912-19	218	42	5.19
1920-29	547	74	7.39
1930-39	440	75	5.87
1940-49	302	105	2.88
1950-59	434	160	2.71
1960-69	264	260	1.02
1970-76	222	341	0.65

^{1/} Annual reports of the B.C. Forest Service give areas burned.

^{2/} Estimated from volumes reported logged.

Recent Fire Losses

In table 2 recent B.C. Forest Service data are summarized to show net areas killed by fire, approximate percentages of area burned, and years required to burn over each fire damage category. Losses in 1976 were much below average. Determination of areas upon which to base percentage losses is necessarily subjective. The B.C. Forest Service Protection and Inventory Divisions use different definitions, e.g., "merchantable" versus "mature," and some classes are not inventoried. The Inventory Division records areas not satisfactorily restocked (NSR), but the Protection Division reports NSR in three categories, logged-not-burned, logged-and-burned, and old-burn-not-logged. For table 2 the base areas assumed for logged-not-burned, and logged-and-burned, are subtracted from the Inventory total to get areas of wildfires burned in NSR that are old-burned-not-logged. Areas of noncommercial cover (NCC) and all forest land are from the most recent Inventory estimates. Areas shown for grazing or pasture land are my estimate of open grasslands and forested ranges currently occupied by domestic livestock. Areas shown for nonproductive sites could support some scrub timber but are not likely to be of commercial value.

The high proportions of area burned in NSR and NCC lands are similar to those reported for the previous decade (Smith 1970a). It is obvious that hazard is highest in recently logged and burned portions of the forest. Hazard as expressed by percentage burn in immature stands is only about 25 percent of that in NSR and is reduced further in merchantable (mature) forests.

TABLE 2.--Areas burned annually in 1967-76 and 1976

Category	Base area ^{1/} <u>M acres</u>	Net area killed by fire				Years to burn all of base area ^{2/}
		1967-76		1976		
		<u>Acres</u>	<u>%</u>	<u>Acres</u>	<u>%</u>	
Merchantable timber	63,385	42,620	0.067	28,338	0.045	1,493
Immature timber	53,086	52,375	.099	15,982	.030	1,010
All not satisfactorily restocked (NSR)	6,641	26,113	.393	19,453	.293	254
NSR logged-not-burned	1,500	14,330	.955	3,488	.233	105
NSR logged-and-burned	500	2,525	.505	575	.115	198
NSR old-burn-not-logged	4,641	9,258	.199	15,390	.332	503
Noncommercial cover (NCC)	4,884	48,430	.992	17,510	.359	101
Grazing or pasture land	10,000	9,660	.097	21,715	.217	1,031
Nonproductive sites	60,000	44,760	.075	33,675	.056	1,333
All forest land	128,749	224,392	.157	142,552	.110	637
All Province	234,403	224,392	.096	142,552	.061	1,042

^{1/} In thousands of acres (M)(405 ha).

^{2/} Assuming percentages burned 1967-76 (col. 3) continue to apply.

Regions Analyzed

Because fire records are maintained by administrative units and reported by Forest Districts, which have changed several times since 1912 when the B.C. Forest Service was established, it is difficult to relate data on fire occurrence and damage directly to bioclimatic zones or forest regions (Rowe 1972). The seven inventory zones applied in the 1957 inventory have been changed to twelve growth zones now being used by the Inventory Division of the B.C. Forest Service. The ecosystem classifications of B.C. also are changing and improving over time (Klinka 1977). Because local altitudinal differences can be so important in relation to broad regional climatic variations, remote sensing is likely to play an important role in determination of refined and "stable" zones. Within 3 years the B.C. Forest Service Inventory Division will have all of its forest cover type "islands" computer mapped and at that time refined analyses of fire occurrence and damage should be undertaken to exploit potentials recognized in 1974 (Smith and Gilbert 1976). For all these reasons only general regional groupings and broad forest cover types based upon tree species are discussed here.

Changes in Proportions of Area by Species Group

One of the most obvious influences of disturbance is the change in species composition that takes place as mature stands are replaced by immature ones. That proportions of Douglas-fir, lodgepole pine, and deciduous species groups have increased greatly and cedar, hemlock, and spruce decreased as a result of wildfires and logging is shown by table 3. The 1957 inventory data (B.C. Forest Service 1958) were summarized by species group, age, and accessibility classes for four periods. Species groups are as defined at the bottom of the table. Two presettlement age classes are shown, the 40 years 1831-70 and all ages before 1831. The period of settlement and urbanization 1871-50 is described by the two 40-year periods before and after initiation of fire control by the B.C. Forest Service.

Although estimated as of 1957, the inventory actually contains data collected by both intensive and extensive methods over a considerable time span. A regeneration delay of from 5 to 10 years following disturbance is common. Therefore, it appeared reasonable to assume that the 1957 data apply best to disturbances up to 1950. The 1957 inventory assumed that deciduous species mature at 41 years, lodgepole pine at 81 years, and all other species at 121 years. Areas of mature deciduous and lodgepole pine stands reported in 40-year age classes were reassigned assuming that 50 percent of the area fell in each 20-year age class.

In each species group (Province, Coast, and Interior) three summaries for accessible forests are given. In addition, all Coast and Interior stands classed as potentially accessible were recorded to help determine the effects of access on species composition and age. In potentially accessible forests, logging would be impeded by difficult topography--locally or along the route over which timber would normally be extracted. Lightning rather than man-caused fires would be most serious in such forests. Differences among accessible forest regions and between them and potentially accessible forests should be of some diagnostic value. It is unfortunate that the 1973 inventory did not provide detailed information on age classes for comparison with the 1957 inventory.

TABLE 3.--Proportion of area by species groups and age classes

Species Age group ^{1/} class ^{2/}	Accessible				Potentially accessible, Province	Species Age group ^{1/} class	Accessible				Potentially accessible, Province
	Prov.	Coast	Int.				Prov.	Coast	Int.		
Percentage of total area in productive forests											
F	1911+	6.3	26.6	4.4	7.3	H	1911+	2.6	12.4	1.6	5.3
	71-10	10.3	21.4	9.9	12.2		71-10	1.5	21.9	0.8	4.4
	31-70	7.0	15.9	6.7	9.0		31-70	2.0	17.7	1.6	4.3
	1830-	4.7	3.1	5.2	1.4		1830-	14.7	30.2	10.7	20.7
FHC PULP	1911+	1.7	16.2	0.3	1.2	S	1911+	26.4	0.3	28.8	31.0
	71-10	0.9	16.2	0.4	2.1		71-10	40.5	0.8	42.0	41.5
	31-70	0.7	12.2	0.4	1.1		31-70	54.4	1.3	55.9	51.8
	1830-	1.8	7.9	0.2	1.1		1830-	55.3	0.9	69.3	58.2
FSB	1911+	0.4	0.1	0.4	1.1	PL	1911+	36.1	1.6	39.3	33.5
	71-10	1.2	0.5	1.3	2.5		71-10	24.3	1.3	25.2	25.6
	31-70	1.7	1.3	1.7	2.0		31-70	27.7	0.8	28.5	22.9
	1830-	1.0	0.1	1.2	0.7		1830-	3.2	0.1	4.0	1.0
FPy	1911+	0.9	0.1	1.0	1.1	Dec.	1911+	17.4	6.4	18.4	7.4
	71-10	1.6	0.2	1.7	0.4		71-10	13.0	2.0	13.4	0.8
	31-70	0.6	-	0.6	1.8		31-70	0.7	1.6	0.7	0.6
	1830-	1.4	-	4.7	0.2		1830-	-	0.1	-	-
FL	1911+	3.5	-	3.9	4.8	All	1911+	21.3	16.3	21.9	10.0
	71-10	2.4	-	2.5	2.4		71-10	25.8	8.4	28.0	13.9
	31-70	1.6	-	1.7	1.5		31-70	13.6	3.3	14.8	9.0
	1830-	0.6	-	0.7	0.2		1830-	39.3	72.0	35.2	67.0
FC	1911+	2.4	21.7	0.7	2.7	All	Area in millions of acres				
	71-10	2.6	21.7	1.9	5.2		1911+	22.2	1.9	20.3	1.4
	31-70	2.2	31.2	1.4	2.5		71-10	26.9	1.0	25.9	1.9
	1830-	1.8	5.9	0.8	1.8		31-70	14.1	0.4	13.7	1.2
C	1911+	2.4	14.7	1.2	4.6		1830-	41.0	8.4	32.6	9.2
	71-10	1.5	13.9	1.0	2.9		All	104.2	11.6	92.6	13.7
	31-70	1.3	18.0	0.9	2.5						
	1830-	15.5	51.7	6.2	15.0						

^{1/}F is Douglas-fir, F pulp includes hemlock (H) and true firs (B), S is spruce, Py is ponderosa pine, L is western larch, C is western redcedar and yellow cedar (Cy), H is hemlock, PL is lodgepole pine, Dec. is deciduous hardwoods (red alder, black cottonwood, birch, and aspen). Scientific names are in Hosie (1969).

^{2/}Acres by age classes reported by the B.C. Forest Service for 1957 were re-sorted to determine the areas and proportions shown for the four periods.

Influence of Species, Site, and Bioclimatic Zone on Plot Mean Ages

For most species (table 4) mean age increases as site quality decreases. For Interior spruce and lodgepole pine ages reported by bioclimatic zones in table 5, plot age also increases as site quality decreases. This may be because poorer sites often are more remote and less attractive for logging because of smaller piece size and lower volumes per acre. Some bias may also have resulted from including only plots supporting trees 7.1 inches (18 cm) d.b.h. and larger (Smith 1976b). Although proportions estimated by ages of plots may differ from those determined by classification of stands, the ages in tables 4 and 5 typify average natural rotations for trees 7.1 inches (18 cm) d.b.h. and larger in important species groups. Because the proportion of defective trees increases with age and decay complicates age determinations, stand classification methods probably would give higher averages than those shown in tables 4 and 5.

TABLE 4.--Influence of site and species on mean age in plots, 7.1 inches (18 cm) d.b.h. and larger, 1972-, Pure Plus Mixed

Species group		Site class ^{1/}								
		1	2	3	1-3	1-3	1	2	3	1-3
		Average Age					Number of plots (NP)			
		All	All	All	All	260+				
F	Douglas-fir	96	115	133	119	287	785	1,760	1,760	4,305
Pw	White pine	67	111	155	125	-	41	56	107	204
Py	Ponderosa pine	63	83	182	139	282	26	34	80	150
L	Western larch	126	109	103	115	291	110	115	48	273
C	Cedar	180	196	223	207	296	27	130	142	299
H	Hemlock	171	191	221	197	285	86	533	231	850
B	"Balsam"	134	168	177	168	281	216	754	756	1,726
S	Spruce	146	167	167	159	293	2,014	2,302	1,135	5,451
Pl	Lodgepole pine	94	104	113	102	271	1,938	1,879	1,100	4,917
Cot.	Black cottonwood	112	101	87	103	-	35	88	11	134
Bi	Birch	-	65	61	63	-	-	22	25	47
A	Aspen	-	76	78	76	-	-	382	84	466

^{1/} Good is 1, medium is 2, and poor is 3.

TABLE 5.--Influence of site and bioclimatic zone on mean age in pure spruce and lodgepole pine plots, 7.1 inches (18 cm) d.b.h. and larger, 1972-

Bioclimatic zone			Site class ^{1/}							
			Spruce				Lodgepole pine			
			1	2	3	1-3	1	2	3	1-3
4	Southwest Dry Belt	Age	169	192	200	187	85	107	112	106
		NP	45	61	37	143	129	223	418	770
5	West Kootenay	Age	136	186	191	169	104	117	118	110
		NP	79	95	50	224	103	75	20	198
6	East Kootenay	Age	235	241	241	239	75	81	93	80
		NP	89	115	54	258	67	66	19	152
7	Central Columbia	Age	184	218	198	200	75	83	98	78
		NP	105	99	18	222	90	47	3	140
8	Nechako-Fraser Plateau	Age	117	135	202	140	93	107	118	106
		NP	57	66	27	150	318	485	328	1,131
9	Central Interior	Age	136	144	140	140	99	104	-	100
		NP	240	223	53	516	201	46	-	247
10	Northwest Plateau	Age	103	125	153	116	96	113	-	99
		NP	27	14	6	47	22	5	-	27
11	Northcentral Plateau	Age	-	137	139	139	-	-	-	-
		NP	-	15	50	65	-	-	-	-
12	Northeastern Plains	Age	137	144	152	144	-	104	82	93
		NP	295	331	246	872	-	41	38	79
4-12	Interior	Age	151	168	169	162	91	105	113	103
		NP	937	1,019	541	2,497	930	988	826	2,744

^{1/} Good is 1, medium is 2, and poor is 3.

Stand Mean Ages and Fire Cycles

Using concepts well illustrated by Van Wagner (1978), it is possible to improve interpretations of percentages of area burned in comparison with those estimated directly from age class distributions for periods, regions, and types. He showed that the annual probability of fire in any one stand, p , the proportion of the whole forest that burns each year, determines the fire cycle, C . The fire cycle is defined as number of years required to burn over an area equal to whole area of the forest, $1/p = C$. Within one fire cycle some stands may not burn and other areas can burn more than once. Van Wagner demonstrated that if fire losses follow the negative exponential distribution, mean age of all stands equals the fire cycle. Also, for the same proportion of forest renewed annually, randomly disturbed forests have twice the average age of regulated forests and many stands greatly exceed rotation age. Van Wagner found that typical types of lodgepole pine-spruce forests in the vicinity of Hinton, Alberta, had fire cycles of 50 years to 1915 and 65 years to 1960.

Since the negative exponential distribution plots over stand age as a decreasing straight line on semilog paper, it provides a convenient basis for examining effects of settlement, urbanization, and improving fire management upon fire cycles in British Columbia. The negative exponential distribution can, of course, be used to describe combined effects of all factors that kill a stand at any age and lead to its eventual replacement. Although the data used here are determined, primarily, by fire and logging, any other factor that leads to the creation of a new forest will be included in the cycles estimated by the negative exponential or other distribution. By removing overmature and mature age classes, logging will bias the fire cycle estimates by superimposing the managed "rectangular" distribution on the random negative exponential distribution.

The 1957 inventory data summarized in table 3 were used to calculate mean ages and fire cycles. Mean ages were determined by multiplying the decimal fraction of the total area in each age class by the midpoint of the class. Fire cycles should roughly equal the mean ages if the negative exponential fits well. Table 6 records mean ages for accessible forests in seven regions, Coast and Interior, and the whole Province. Data were available for only one potentially accessible class that combines Coast and Interior forests. Periods represented are settlement and urbanization, 1950-, and presettlement, 1870-. For the 1950- period, estimates are made first including and then excluding the proportion of NSR and NCC as a zero age class. Areas for each region are given in millions of acres (405 thousand ha). Excluding the zero age class increases mean age by 39 years on the Coast and 14 years in the Interior. Because three classes have lower mean ages in the presettlement period, 1870-, than in the period 1950- including zeros, suggests that improving forest protection reduced losses in all potentially accessible types and in accessible portions of the Northwest Interior and Northeast Interior. Comparing mean ages of 1870- with those of 1950 in which zeros are excluded adds the North Coast and North Central Interior as regions which also might have had areas burned reduced modestly by improved protection. Another interpretation is that mean age of Coast forests was reduced from 262 to 228 by logging and wildfire, while the mean age of Interior forests was increased from 92 to 102 by improved protection.

Estimates of fire cycles are made by plotting percentages of total area found in each 20-year age class over age at the midpoint of the class. With the exception of the South Central Interior, lengths of fire cycles exceed mean ages, for 1950- including the zero age class. Data for potentially accessible stands were plotted using the estimated Interior average age of 300 years for overmature timber. For 1870-, proportions of area in zero age classes obviously could not be determined. Proportions were recalculated and age class midpoints reduced by 80 years, with the exception of the overmature class which was plotted as 295 for the Interior and 420 for the Coast. From

TABLE 6.--Mean ages and fire cycles for forest regions of B.C.

Period	Pot. acc. ^{1/}	Accessible										NSR NCC ^{2/}
		Coast	Int.	Prov.	NC	SC	NWI	NCI	SCI	SEI	NEI	
<u>Mean age, years</u>												
1950-	154	189	88	81	231	176	129	75	71	78	75	Incl.
1950-	160	228	102	116	264	215	160	120	97	101	82	Excl.
1870-	131	262	92	109	240	272	114	106	107	105	60	Unknown
<u>Fire cycle, years</u>												
1950-	136	234	85	94	192	244	134	102	74	82	68	Incl.
1870-	86	128	63	96	116	139	74	72	79	72	42	Unknown
<u>Area, million of acres (405 thousand ha)</u>												
All	14	14	109	123	3	11	8	32	14	14	41	Incl.
All	14	12	92	104	3	9	6	27	10	11	38	Excl.

^{1/} Potentially accessible, for all regions, Coast, Interior, Province, North Coast, South Coast, Northwest Interior, North Central Interior, South Central Interior, Southeast Interior, and Northeast Interior.

^{2/} Areas classed as not satisfactorily restocked (NSR) and noncommercial cover (NCC) as well as partially logged (residual) stands are included or excluded as the zero age class. Such areas are not known for 1870 and earlier.

common logarithmic graphs, rates of annual decrease in percentage area burned were converted to natural logarithmic rates in order to satisfy requirements of the negative exponential distribution.

Van Wagner (1978) modified the approach of Johnson and Rowe (1977) to show how the Weibull could be used to account for variation in flammability with time. Means from the Weibull formula were calculated first for the Province, Coast, and North and South Coast regions in table 6 and for the hemlock and cedar types of table 7. During this process estimates of means (fire cycles) from the negative exponential and Weibull were similar, where the negative exponential applied. Subsequently, means were calculated by the Weibull for Coast, Interior, and Potentially Accessible classes of table 7. In most cases fire cycles defined by the Weibull were similar to those obtained from graphing on semilog paper. Because application of the Weibull provided estimates for cases that could not be solved using the negative exponential function, and because mathematical fitting provides better and more objective fits, general use of the Weibull is the preferred method. Some complications will arise from assumption of an average age of 300 years for overmature Provincial and Potentially Accessible types which leads to minor anomalies in comparisons with Coast and Interior regions and types.

Influence of species groups on mean ages and fire cycles within major forest regions can be determined from table 7. Zero age classes were excluded because it was not possible to distribute them among species groups. Mean ages of Douglas-fir and spruce types are similar. Cedar and hemlock types are much older and lodgepole pine and deciduous types much younger than average. The fire cycle could not be determined from plots on semilogarithmic paper for Douglas-fir, spruce, cedar, and hemlock, so their mean was estimated from the Weibull formula. There is excellent agreement for the fire

TABLE 7.--Mean ages and fire cycles for major forest regions and species groups, excluding zero age class

Region	Period	Species group										
		F	F pulp	FS	FPy	FL	FC	C	H	S	PL	Dec.
		Mean age										
Prov.	1950-	95	143	113	118	64	112	213	195	119	64	38
	1870-	91	179	70	116	73	136	194	162	86	67	40
Coast	1950-	97	185	81	104	-	144	278	251	188	59	49
Int.	1950-	97	83	70	118	64	100	182	180	118	64	37
Pot. Acc.	1950-	94	168	113	109	60	149	156	208	153	66	23
Fire Cycle												
Prov.	1950-	98	132	147	127	108	96	185	168	109	57	16
	1870-	92	254	48	99	75	131	-	-	69	65	36
Coast	1950-	95	186	-	-	-	132	205	202	-	79	26
Int.	1950-	78	81	147	107	52	79	161	155	103	49	20
Pot. Acc.	1950-	75	254	-	-	-	152	259	205	131	53	17
Area, Millions of Acres (405 thousand ha)												
Prov.	1950-	7.1	1.4	1.1	1.3	1.9	2.3	7.4	7.3	47.1	19.8	7.5
Coast	1950-	1.0	1.1	-	-	-	1.2	4.8	3.1	0.1	1.0	0.2
Int.	1950-	6.1	0.3	1.0	1.3	1.9	1.1	2.6	4.2	47.0	19.7	7.3
Pot. Acc.	1950-	0.6	0.2	0.1	0.1	0.1	0.3	1.5	2.1	7.2	1.3	0.1
Fire Cycle Acceptable to Beall (1949)												
Coast		909	1,000	-	-	-	1,000	1,176	1,000	1,250	-	667
Int.		454	-	-	-	944	-	667	667	667	500	400

cycle in Interior lodgepole pine, 1950, and that estimated by Van Wagner (1978) for the lodgepole pine-spruce forests near Hinton, Alberta. Mean ages and fire cycles for all species groups and the periods 1950-, and 1870-, are much less than the fire cycle which would have been acceptable to Beall in 1949. By converting his percentages of area burned annually to approximate fire cycles, it can be seen that cycles in table 7 are much less than the standards proposed by him.

RESULTS OF INTENSIFIED FIRE CONTROL

Although analyses for tables 6 and 7 showed that the negative exponential function did not always fit, it is useful to assume that it does apply in order to consider the impact of intensified fire control 1950-73 on fire cycles. If the fire cycle is the reciprocal of the fraction of the area burned annually, it is obvious that there has been a recent and great improvement in fire control. That is expressed by an apparent fire cycle of 1,042 years for 81.126 million acra (32.831 million ha) in table 8. The table records percentages of Public Sustained Yield Unit areas burned annually in mature and immature stands in each of 15 growth types. The worst type, No. 2 (FC, FCy, FH and FS) has a fire cycle of 112 years in mature and 351 years in immature stands, probably as a result of high slash hazards. The most fire-resistant type is rather surprising since it required disturbance for establishment; the deciduous

hardwoods in growth type 15 have a fire cycle of 100,000 years. These data confirm DeByles's (1978) observation that pure aspen stands provide natural firebreaks and are difficult to burn even under extremely dry conditions.

Data in table 8 show a remarkable change from previous tables in the proportion of types classed as spruce. There are only 18.2 million acres (7.4 million ha) of pure and mixed spruce types in table 8. Replacement of aerial reconnaissance with intensive sampling and recognition of true firs as commercial species took place between the 1957 and 1973 inventories. Adding the area in true firs (growth type 8) which would have been classed as spruce in 1957 brings the total to only 27.3 million acres which still is proportionately much less than the 47.1 million acres (19.061 million ha) analyzed for table 7.

Table 9 records estimates of fire cycles from percentages burned annually 1950-73 by 12 bioclimatic regions. The worst fire losses are in the Northwest Plateau (125-year cycle) and in the Northeastern Plains (202-year cycle). The North and Central Coast region has a fire cycle of 5,263 years estimated from losses 1950-73. Further analyses are needed to relate fire occurrence to climate 1950-73 in comparison with long-term averages. There is a useful relationship between amounts of spring and summer precipitation and number of fires (Smith 1970) which could be analyzed with hours of sunshine to determine whether or not climate 1950-73 was typical.

With the exception of the Northwest Plateau, the fire cycle 1950-73 is so long that if it persists fire would no longer be a major source of disturbance and forest renewal.

Although fire control has improved greatly, it is difficult to estimate what might happen if there is a repetition of the seasons in which million-acre fire years occurred. The worst recorded fire years in terms of millions of acres (405 thousand ha) burned were 1922 with 1.6, 1929 with 1.0, 1931 with 1.0, 1940 with 0.5, 1958 with 2.1, 1961 with 1.2, and 1971 with 0.9. Fire control organizations must be manned, equipped, and financed to handle such extreme years.

In table 10 some other important dimensions of wildfires are reported for the bioclimatic regions. Fire occurrence is least in the remote, undeveloped North-central Plateau and greatest in the heavily settled and dry West Kootenay region. The strong association between number of fires reported and their size and damage caused suggests that many fires in the remote regions may not have been large enough to attract attention.

INFLUENCES OF RESEARCH ON FIRE MANAGEMENT DECISIONS

Considering the small effort devoted locally to fire research, the lack of professional fire managers, and the huge logistic problems in the vast area of British Columbia, there has been good progress in creation and application of knowledge to improve fire management. Results of research that can be seen as having good chance of improving practical fire management are eagerly applied.

New technology and improved equipment have been introduced at all levels to speed fire control and reduce labor inputs. Use of airplanes for detection and water bombers and helicopters for suppression have increased costs but made control much faster and more effective. Fire-danger ratings and methods for determining when to burn slash have been widely applied. Guidelines have been made objective and slash burning seasons have been extended to safe periods in spring and summer as a result of research. Worries about air pollution, soil damage, and depletion of nutrients, some spectacular escaped slash fires, and improved markets for small logs and defective timber have reduced areas broadcast burned. Methods for prompt ignition of slash fires have been applied widely. Recognition of the natural role

TABLE 8.--Percentage area burned annually 1950-73 and fire cycle by growth type

Growth type	Species and Region, Coast (C) Interior (I)	Fraction burned annually and fire cycle						Area M + I M acres
		Mature (M)		Immature (I)		M + I		
		%	Years	%	Years	%	Years	
1	F, FPL(C), F Dec., PwC	0.108	926	0.073	1,370	0.091	1,099	3,718
2	FC, FCy, FH, FS	.893	112	.285	351	.511	196	1,242
3	FPL(I), FPy, Py, F Dec. (I)	.199	503	.190	526	.194	515	1,708
4	FL, Pw(I), LF, L	.193	518	.107	935	.126	794	1,375
5	C, CF, CH	.022	4,545	.246	407	.032	3,125	3,552
6	H, HPL, H Dec.	.088	1,136	.021	4,762	.007	14,286	1,202
7	HF, HC, HB, HS	.179	559	.127	787	.173	578	4,078
8	B, BH, BS	.015	6,667	.025	4,000	.017	5,882	9,087
9	S	.044	2,273	.094	1,064	.065	1,538	6,785
10	SF, SH, SC, SB	.150	667	.092	1,087	.140	714	6,350
11	SPL, S Dec.	.217	461	.381	262	.315	317	5,068
12	PL	.023	4,348	.090	1,111	.062	1,613	21,997
13	PLF, PLS, PLB	.089	1,124	.260	385	.173	578	5,731
14	PL Dec.	.001	100,000	.002	50,000	.002	50,000	1,266
15	D Dec., Mb, Bi, A Dec.	.001	100,000	.001	100,000	.001	100,000	7,967
1-15	All	.083	1,205	.112	893	.096	1,042	81,126

TABLE 9.--Fire cycle 1950-73 by bioclimatic regions

Bioclimatic region		Fire cycle from percentages burned annually by cover type			
		Merchantable	Immature	Other ^{1/}	All
		<u>Years</u>			
1	North and Central Coast	50,000	1,351	4,348	5,263
2	Southern Coast	14,286	3,333	1,351	1,266
3	South Coast Transition	1,786	699	625	781
4	Southwest Dry Belt	1,449	1,266	485	926
5	West Kootenay	3,333	3,448	893	2,083
6	East Kootenay	1,190	1,163	1,190	1,124
7	Central Columbia	571	1,190	613	645
8	Nechako-Fraser Plateau	2,632	592	493	775
9	Central Interior	2,439	5,556	725	1,408
10	Northwest Plateau	296	226	101	125
11	Northcentral Plateau	1,370	1,818	446	685
12	Northeastern Plains	926	794	1,437	202

^{1/} Nonforest, residual, NSR, and NCC.

TABLE 10.--Occurrence, size, and damage caused by wildfires 1950-73 by bioclimatic regions

Bioclimatic region	No. fires annually	Area	Damage
	<u>Per million acres</u>	<u>Per fire acres</u>	<u>Per fire dollar</u>
North and Central Coast	2.1	93.7	706
Southern Coast	7.3	53.2	934
South Coast Transition	27.5	46.9	861
Southwest Dry Belt	41.9	25.7	243
West Kootenay	42.8	11.3	301
East Kootenay	23.7	37.2	584
Central Columbia	23.2	66.6	1,337
Nechako-Fraser Plateau	9.3	139.2	1,906
Central Interior	9.5	74.8	966
Northwest Interior	7.0	1,149.0	5,139
Northcentral Plateau	0.8	1,796.6	11,974
Northeastern Plains	2.9	1,691.3	6,271

of fire in reducing accumulations of fuel and encroachment of trees on grasslands have stimulated prescribed burning to create and maintain habitats desired by managers of wild and domestic animals. Fire lines have been constructed by blasting. Arguments for and against reservation of mature timber as firebreaks have been evaluated and recognition is growing that they are expensive and not likely to be efficient. Hazards associated with thinning have been analyzed. Simulators have been used to improve fire-control training. Public awareness of the need for care with fire has been enhanced while admitting that there is an important natural role for fire in many ecosystems.

As a result of recent enthusiasm for maintaining and enhancing environmental quality, ecological approaches to writing prescriptions to use fire (Klinka 1977) have been viewed with increased interest. Field foresters seeking to reduce soil damage have paid more attention to ecologists than to economists. "Sensitive" soils are being withdrawn from timber production or logging in Environmental Protection Areas.

Although research to quantify fire damage has grown and results of mathematical modeling and simulation have been applied operationally, there have been too few attempts to apply economic theory to reduce costs, enhance benefits, and optimize the allocation of resources. There has been good presuppression planning, but the general lack of standards and of formal fire control planning is regrettable.

OPTIONS FOR MODERN FIRE MANAGERS

In addition to recognizing the effects of fire, logging, and other disturbances on species composition, lengths of fire cycles should be considered carefully in relation to fire management objectives. Data on mean ages and fire cycles of stands established before settlement and urbanization indicated that fires average once a century. The fire cycles 1950-73 resulting from improved protection are now so long in relation to those in presettlement forests that the need for further improvements is not obvious. It is remarkable that the fire cycle estimated for all types in tables 2 and 8 is the same, 1,042 years. For the Province as a whole, more favorable weather and/or better fire control methods have made the apparent fire cycle nearly 10 times longer in 1950-73 than it was in the presettlement period 1870-. Average area burned annually since 1950 is considerably lower than that considered "acceptable" by Beall (1949). Now that capacity to achieve desirably long fire cycles and associated low percentages of area burned annually has been demonstrated for several decades, attention should be shifted to definition of optimum age class structures for natural and managed forests.

Since natural fire cycles can be estimated from age class structures determined by conventional forest inventories, studies should be undertaken for each timber supply area and evaluated in association with analyses of fire-scarred trees to determine frequency of sublethal as well as killing fires.

The alternatives open to fire managers are to do nothing, to do the same as present, to change protection efforts to achieve desired standards, to reassign protection efforts to give the most protection to resources of highest value, or to respond cooperatively to a gradual shift of budgets toward action on new opportunities which may have higher benefits than traditional fire control. In order to accomplish beneficial changes, better information about potential costs and benefits will be needed. Productivity in application of fire-control techniques must be determined and considered carefully. Reintroduction of the natural role of fire must be given the attention it deserves.

Recently, as evident in papers presented at this conference, valuable progress has been made by the USDA Forest Service and other agencies toward comprehensive definition and quantification of options open to fire managers. New policies which

take a more positive approach to fire have been advocated by Gale (1977) who urged recognition of the natural role of fire in ecosystems and the need for firm association of suppression objectives with resource management goals. Barney (1978) has developed a process to integrate fire with land-use planning and management activities. Impressive advances in concepts and methods for integration of fire management into land-use planning are being made under the direction of Lotan (1979).

Although there is growing recognition of benefits from tolerating wildfires on some habitats, or from purposeful introduction of fire, these must not be allowed to diminish development of improved fire-control capabilities. Fire managers must have good initial attack capabilities, and where initial attacks fail, sufficient backup to deal with several large fires simultaneously. At all times good fire management must involve the capability to control prescribed fire when conditions change or prescriptions prove faulty.

On most problems much more research is needed. Although prescribed fire has a potentially important role in controlling dwarf mistletoe (Muraro 1978a) and in thinning lodgepole pine (Muraro 1978b), it takes much effort to translate sound theory into effective operations.

CONCLUSIONS

Recognition of the role played by wildfires in all British Columbia forests prior to settlement and knowledge of the impacts of wildfire, land clearing, and logging in the settlement and urbanization period are increasing. In addition, there are some studies indicating incidence of sublethal wildfires on a cycle of 10 to 15 years before the period of intensified fire control in the Interior of B.C. As fire control has improved, the natural fire cycle of about 100 years has lengthened to recently indicated cycles of about 1,000 years. Since 1950, areas burned have been held to levels that can be considered as acceptable to timber managers.

Now that a capacity for satisfactory fire control has been demonstrated, timber managers and other resource managers can feel more comfortable about investigating the possibility of returning sublethal wildfires to their natural levels in types where net benefits will result. The negative exponential and Weibull frequency distributions can provide help in defining desirable distributions of age classes to be maintained in natural forest, and in estimating effects of all sources of disturbance leading to renewal of stands in managed forests. Researchers have indicated many potentially interesting alternatives that merit careful consideration by fire managers.

Although research is needed to improve all aspects of fire control, much more effort should soon be directed to thorough analyses of fire benefits as well as fire damage. Standards which are well founded in economic as well as ecological considerations should be developed and applied. With greater emphasis on cost effectiveness and increased concern for intensive timber management, some of the resources assigned traditionally to fire control may be better spent in control of other pests, in other regions, and in quite different ways.

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REGIONAL IMPACTS OF FIRE

Arthur R. Tiedemann

Supervisory Range Scientist
USDA Forest Service
Intermountain Forest and Range Experiment Station
Provo, Utah

ABSTRACT

Increased emphasis on prescribed burning as a forest management tool and new fire management policies of public agencies have set the stage for increased conflict between fire and humans. This paper attempts to identify and characterize some of the more significant offsite effects of wild and prescribed fire as related to frequency and intensity and to evaluate the relationship between basic research and policies established for preventing or minimizing unacceptable offsite consequences. Topics considered are the effects of smoke and other products of combustion, and the effects of fire on esthetics, recreation, watershed, and the economy.

KEYWORDS: fire effects, fire frequency, fire intensity, air quality, recreation, local economy, regional economy, water quality, soil erosion, aquatic habitat.

INTRODUCTION

In the last two decades we have witnessed a striking increase among wildland managers in prescribed burning as a management option for abating fuel hazards, regenerating the forest, and altering vegetative composition of forest and range habitats for a variety of purposes. Interest has been spurred by revision of policies of fire management and strategies for public lands. Kilgore and Briggs (1972) described the revised policy for the National Park Service, U.S. Department of the Interior, whereby natural fires are recognized as natural phenomena, allowed to run their course when they can be contained within predetermined fire management units, and will contribute to accomplishment of approved vegetation and/or wildlife management goals. The policy also provides for prescribed burning to obtain these goals.

Concern for natural and human-caused accumulation of forest fuels and the possibility of eventual destructive conflagrations (Gale 1977) recently resulted in change in the fire management policy in the Forest Service, U.S. Department of Agriculture, "to allow variable fire suppression based on land management objectives and the values at risk in areas of consideration."^{1/}

Greater use of prescribed burning and new public land fire-management policies, coupled with rapid expansion of population centers into wildland areas, provide the elements for conflict between people and fire. Concern for offsite effects--such as loss of life from floods originating in burned watersheds, pollution from smoke, deterioration of water quality, and economic losses--may be manifested in the development of guidelines, policy statements, and laws that regulate adverse activity on the land.

In this paper I will attempt to identify and characterize some of the more significant offsite effects related to frequency and intensity of fire. My second goal is to demonstrate the relationship between basic research and policies established for minimizing or preventing unacceptable offsite consequences.

The major offsite considerations are effects of smoke and other products of combustion and effects of fire on esthetic and recreational values, local and regional economic values, and watershed attributes.

OFFSITE EFFECTS OF SMOKE AND COMBUSTION PRODUCTS

Smoke, the visible product of the incomplete oxidation of plant materials by combustion, is an immediate and obvious contributor to a variety of offsite effects. Much information has been published on the process of combustion and the resultant products that have a potential for creating pollution (MacArthur 1966, Fritschen and others 1970, Murphy and others 1970, J. A. Hall 1972, Darley and others 1973, Hruza and others 1974, Tangren and others 1976, McMahon and Ryan 1976). Discussion of the physiochemical mechanics of combustion and emission processes in burning are beyond the scope of this paper.

I will attempt to summarize the more significant aspects of emissions from forest fires (wild and prescribed) as air pollutants and as contributors to other offsite effects. Some effects, such as impairment of visibility and human health problems, are relatively obvious; whereas effects of light attenuation by smoke on ripening of fruit and effects of smoke on adjacent plant communities may be very subtle.

Air Quality

J. A. Hall (1972) concludes that the principal objection to results of prescribed burning is temporary interference with visibility. Smoke from large wildfires in the West has affected visibility as far away as New York State (Schlapfer 1976), and there are numerous accounts of local visibility problems created by smoke from wildfire and prescribed fire. Some are very serious. Mobley (1974) cites a situation in Florida in which smoke blanketing a highway caused a pileup of cars that resulted in five deaths and numerous injuries.

^{1/} U.S. Department of Agriculture, Forest Service. 1978. Revised fire management policy fact sheet adapted from Forest Service manual, FSM 5100 Fire Management Amendment 56.

The principal pollutants from burning of forest fuels are carbon monoxide (CO), carbon dioxide (CO₂), particulates, nitrogen oxides (NO_x), and hydrocarbons (Fritschen and others 1970, J. A. Hall 1972, Darley and others 1973, Cooper 1974, McMahon and Ryan 1976, Tangren and others 1976). Most of these authors agree that particulates are the principal air pollution problem. Tangren and others (1976) define particulate matter as "any displaced aggregate matter, solid or liquid (other than water) that for practical purposes is larger than about 0.002 microns but smaller than 500 microns." Size, shape, porosity, density, and other physical properties are highly variable.

Suspended particulate matter (less than 5-10 µm) is transported long distances and has the greatest potential for impact on the environment. J. A. Hall (1972) estimates annual emissions of particulates from prescribed fire and wildfire in the United States at 6.1 million metric tons. According to Ward and others (1976), emission estimates vary from 0.45×10^6 to 49×10^6 metric tons per year. Forest fires account for nearly 24 percent of the total particulates produced from all sources (Dieterich 1971). Of the total production of particulates, wildfires account for 90 percent because of greater number of hectares burned and higher amounts of emission than prescribed fires (Ward and others 1976).

Sandberg and Martin (1975) characterized particulate emissions from burning Douglas-fir (Pseudotsuga menziesii Mirb. Franco) logging residues. The most abundant particles were smooth and spherical, ranging from less than 0.05- to 80-µm (1 µm = 1 micron) agglomerates. A second group was classified as polydisperse and ranged from infinitesimal size to 20 µm.

In addition to obscuring visibility, particulates from forest fires have a potential for causing human health problems. Tangren and others (1976) indicate that the sorptive powers of smoke particles for toxic materials, coupled with their minute size, is conducive to depositing toxic materials deep in the lungs. Formaldehyde, for example, does not readily penetrate the upper respiratory tract but may be carried to the lungs by adsorption of smoke particles and may thereby increase its toxic effectiveness (Engel and others 1971).

Natural ambient air quality standards (NAAQS) for particulates have been promulgated by the Environmental Protection Agency. According to Coleman (1976), the primary standard to be obtained within 3 years after the standard is set is a maximum of 260 µg/m³ in 24 hours and an annual geometric average of 75 µg/m³. The secondary standard to be attained within a reasonable time is a maximum of 150 µg/m³ in 24 hours and an annual geometric average of 60 µg/m³, to be used as a guide in achieving the 24-hour standard. The secondary standard to be attained within a reasonable time is a maximum of 160 µg/m³ in 24 hours and an annual geometric average of 60 µg/m³ to be used as a guide in achieving the 24-hour standard. Definition of a reasonable time depends upon the type of control possible, cost of control, and other factors peculiar to the geographical area. Coleman indicated that determining effects of particulates on human health is complicated by the presence of other pollutants, particularly sulfur dioxide (SO₂). Since forest fires emit only trace amounts of sulfur oxides (J. A. Hall 1972, Cooper 1974), the interaction of particulates and SO₂ would be expected to pose a health hazard mainly in areas with a high level of SO₂.

Carbon monoxide and NO_x are the other principal emissions from fires that have a potential for direct effects on human health. Carbon monoxide is very toxic; levels exceeding 10 p/m for prolonged periods have potential for an adverse effect on warm-blooded animals (Horvath 1973). The Environmental Protection Agency has set 35.0 p/m as the primary standard (1-hour annual maximum) and 9.0 p/m as the secondary standard

(8-hour annual maximum) (Federal Register 1971). Although CO levels may exceed 8,000 p/m in the flame (Fritschen and others 1970) and 200 p/m at firelines (Tangren and others 1976), levels are generally diluted to those of ambient air levels within very short vertical and horizontal distances (<100 m) from fire (Fritschen and others 1970, Tangren and others 1976). Although Countryman (1971) concluded that a CO hazard exists for workers exposed to smoke for prolonged periods at firelines, Dieterich (1971) and J. A. Hall (1972) stated that there is very little hazard to public health from CO from forest fires. Dieterich pointed out that a longer term effect from CO that is worthy of consideration is its importance in atmospheric reactions that create photochemical smog.

J. A. Hall (1972), Cooper (1974), and Cramer (1974) do not consider nitrogen oxides to be important emission components from forest fires or prescribed burns. In contrast, Tangren and others (1976) feel that information on NO_x emissions from forest fires is "scanty and inconclusive." They further contend that importance of NO_x to people probably lies in the formation of secondary products.

In addition to emissions discussed above, forest fires generate numerous hydrocarbon compounds, characterized by Fritschen and others (1970), J. A. Hall (1972), and McMahon and Ryan (1976). These compounds may react with sunlight to form photochemical smog (Darley and others 1966). In Australia, Evans and others (1974) showed that irradiation of emissions produced by burning eucalyptus created an ozone layer with a concentration of 0.1 p/m that would have been hazardous if it had reached ground level. The ozone was, however, confined to a shallow layer at the top of the plume, 1,000 m above the ground. Along with the health hazard potential of photochemical smog, Dieterich (1971) expresses concern for the largely unknown synergistic effects of combining two or more chemicals, whereby the resultant compound may be more toxic to humans, animals, and plants than any of the individual chemicals.

Responses of Adjacent Forest Areas and Agricultural Crops

Effects of smoke on adjacent forest communities and agricultural areas are not well documented but may be important offsite considerations because of potential effects on forest productivity and agricultural crops.

Parmeter and Uhrenholdt (1976) found that smoke from wildfires and prescribed fires may create conditions unsuitable for germination of spores of several kinds of fungi. They point out that results suggest that smoke in forests may have important effects on microbial activities, such as initiation of disease, nutrient cycling, mycorrhizal development, and other processes that influence development of plant communities.

Smoke alters both the intensity and quality of light reaching forests and agricultural crops. Fowler^{2/} has shown that radiation flux is more strongly attenuated by smoke in wavelengths of 200-500 nm than at 600-700 nm. Photosynthesis and a variety of other plant physiological processes would be expected to be affected by attenuation of light at both of these wavelength ranges.

Protracted periods of heavy smoke may be especially undesirable in some areas, such as the fruit-producing Yakima and Wenatchee Valleys of Washington State where fruit dominates the economy. Schrader and Marth (1931) found that shading apple trees with cheesecloth and muslin with reductions of 39 to 81 percent of full intensity

^{2/}Personal communication from Dr. William B. Fowler. Principal Meteorologist, USDA Forest Service, Forest Hydrology Laboratory, Wenatchee, Wash.; information is from an unpublished manuscript, "The Effect of Aerosol Concentration with Height on the Intensity and Spectral Balance of the Direct Solar Beam."

resulted in smaller apples having poor color development compared to apples from trees growing in full sun. Seeley and others ^{3/} have recently shown that Delicious apples grown in low-light environments (0.2 to 37 percent of full sun) had lower starch and soluble solids than those grown in full sunlight. Of particular interest was that attenuation of the 400- to 700-nm incident radiation received by fruits and leaves affected color, soluble solids, starch content, and size of the fruit.

Although results of these studies were not directly related to effects of reduced illumination caused by smoke, they do indicate a potential, heretofore unquantified, offsite effect of fire which needs to be more carefully considered.

Some of the chemicals released by the combustion process should also be viewed from the perspective of their potential for enriching the nutrient capital of adjacent or downwind forest and agricultural areas. The combustion process releases large quantities of plant nutrients that are in the intrabiotic stage of the soil-plant-soil cycling continuum. Losses of nutrients occur through either volatilization or convection of ash. Ash is comprised principally of oxides of the metallic elements calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na).

Nitrogen (N) appears to be particularly susceptible to loss during combustion. Studies of various litter and plant materials under controlled conditions show losses between 25 and 60 percent of the total N contained in such material (Debell and Ralston 1970, Wells 1971, Lewis 1975). Nitrogen loss begins at 200°C (White and others 1973) and increases to about 60 percent at 700°C (Knight 1966). Lewis (1975) showed that organic-N compounds, nitrite-N, and ammonium-N, are present in significant amounts in smoke from burned pine litter; however, he detected no nitrate-N (NO₃-N).

Estimates of N loss range from 72 kg/ha (Lewis 1975) to 855 kg/ha (Grier 1975). Grier also estimated losses of Ca, Mg, Na, and K of 75, 33, 282, and 698 kg/ha from a Douglas-fir forest in eastern Washington. Old-field burns in southern Ontario, Can., resulted in losses of K, Ca, Mg, and P ranging from 28 to 62 percent of that contained in the biomass (Smith and Bowes 1974). They felt that most of the loss occurred as fly-ash since burns were of low intensity with surface temperatures not exceeding 500°C. Approximately 30 percent of nutrients lost were recovered in the first 40 m downwind from burned areas.

Clayton (1976) measured the input of nutrients to areas adjacent to watersheds being burned by wildfire. Concentrations of Ca, Mg, K, Na, and N in precipitation falling through smoke during a forest fire were 20 to 70 times greater than in normal precipitation. Dry and wet deposition comprised 1 to 4 percent of the annual nutrient gain to a watershed adjacent to a burned area. Clayton concluded, however, that redistribution of nutrients by smoke is of little ecological significance away from the burned sites--even with the high frequency of fire in the central Idaho mountains.

Atmospheric Effects

Among the more subtle and potentially protracted effects of fire are those exerted on the global heat balance as a consequence of increased particulates and CO₂ concentrations and on precipitation amount and distribution because of increased particulates.

^{3/} Personal communication from Dr. Earl Seeley, Washington State University Tree Fruit Research Center, Wenatchee, Wash.; information is from an unpublished manuscript, "Delicious Apple Fruit Size and Quality Are Influenced by Illumination Level," by E. J. Seeley, W. Micke, and R. Kammereck.

Cramer (1969) speculated that increased particulates in the atmosphere functioning as cloud condensation nuclei (CCN) might result in greater numbers of small droplets that might not grow large enough to fall as precipitation.

Warner (1968) examined 60 years of rainfall for the cane harvest season along the eastern Australian coast. A reduction in rainfall at inland stations coincided with increased production of sugarcane and burning of canefields, but rainfall was not reduced at a control station upwind of smoke. Warner concluded that the reduction was consistent with the hypothesis that smoke particles through their activity as CCN cause smaller droplets which hinder coalescence and formation of rain. Hobbs and Radke (1969) observed about tenfold increases in concentration of CCN at 2.5 km downwind from a 12-ha slash fire; this indicated that burning generates large concentrations of CCN active at about 1-percent saturation.

Relationship of Smoke to Fire Frequency and Intensity

The relationship of frequency and intensity of forest fire to offsite effects from smoke and other products of combustion is a highly controversial issue because of standards promulgated by the Environmental Protection Agency and problems created by smoke. The problem is complicated by difficulties in determining effectiveness of fuel hazard abatement in reducing total smoke emissions. Cramer (1974) pointed out that great variation from year to year of weather, lightning storms, and periods of strong winds makes actual quantification extremely difficult. He concluded, however, that wildfires have decreased in all forest areas and the result has been an accumulation of fuels that increase chances of pollution caused by smoke from large wildfires. He attributed the reduced amount of acreage burned by wildfire in the South to increased use of prescribed fire. In the Pacific Northwest, alternate means of slash disposal and fuel hazard abatement, coupled with increased efficiency in fighting fire have reduced wildfire acreage. It appears that the outcome of a vigorous prevention and suppression program for unmanaged forest areas is a continual buildup or accumulation of fuels and an eventual inevitable series of conflagrations (Gale 1977). According to Cooper (1974), air quality in the southern United States has not deteriorated more where prescribed fire is used extensively than where it is not used. The amount of fuel consumed by wildfires is about three times greater than by prescribed fire for the same area burned and particulate emissions may be 10 times greater (Ward and others 1976). The reason for lower emissions from prescribed burning is that this type of fire mainly consumes fine fuels with high surface area to volume ratios that ignite readily and are more completely combusted (Cooper 1976). Intensities in wildfires are greater than in prescribed fires. Consequently, larger fuels with lower surface to volume ratios and poorer combustion efficiencies are burned, resulting in greater particulate emission than from prescribed fire.

Fritschen and others (1970) concluded that "air pollution aspects of slash burning can be minimized by a high energy release rate fire with a strong convection column under conditions favorable for rapid atmospheric dispersion. The fire should be of short duration to consume the smaller fuels only."

It appears from the literature reviewed that for many wildland areas of the United States, prescribed fire properly planned and executed has great promise as a means to reduce or control smoke pollution problems.

Relationship of Basic Research to Policy Formulation

There is no apparent direct relationship of basic forestry research to policy formulation regarding emissions from forest fires. Dahl and others (this volume) in another paper of this session describe in detail the evolution of fire management policy in the United States. Human health aspects appear to be the most important consideration in the development of National Ambient Air Quality Standards.

Promulgated limits are based principally on results of tests with laboratory animals, human postmortem studies, and tests of human tolerances as described by Einhorn (1976). The Clean Air Act of 1970 (U.S. Laws, Statutes, etc. 1970)--coupled with concern at the State level for pollution from forest fire, agricultural burning, and mill-waste burners--has resulted in individual State programs whereby nonconforming burning activities may either be prohibited or controlled as to timing and magnitude. Programs for Montana, Oregon, and Georgia are described by Neilson (1976), Patterson (1976), and Collom (1976), respectively. The most significant contribution of basic forestry research to the problem of emissions from forest fires has been advanced technology for burning effectively to achieve forest management objectives and still conform to laws regulating smoke and other pollutants. The "Southern Forestry Smoke Management Guidebook" (Mobley and others 1976) is a superb example of the application of basic research to control smoke emanating from prescribed fires. This document provides the forest land manager with the necessary knowledge to achieve reduction of fuel hazard and vegetation conversion objectives while maintaining acceptable levels of ambient air quality.

ESTHETIC AND RECREATIONAL EFFECTS OF FOREST FIRE

Effects on esthetics and recreation are probably the most elusive and nebulous offsite effects of fire to characterize because human attitudes are involved--attitudes that are a combined response to previous experience, education, and other external stimuli. According to A. D. Hall (1972), attitudes stem largely from the sub-conscious mind. He concludes that even though attitudes toward forest fire vary almost infinitely, it is a widespread opinion that fires are harmful and do a great deal of damage. The more directly a person is involved or affected through loss of income, destruction of property, or loss of place of recreation, the stronger are his feelings against fire. Hall does present, however, an optimistic view that there is increased awareness and appreciation among the general public for the natural role of fire.

Stanley (1932) was concerned about the effects of forest fires on tourism in resort areas of northern California. Even in the 1930's, tourism was important enough to have generated revenues comparable to those of agriculture, livestock, and mining. Forest fires were shown to exert a striking negative effect on tourist travel. Stanley cites two principal reasons: people were afraid of being drafted to fight fire, and smoke creates unpleasant conditions for recreation. He also felt that fires ruin pleasant recreation areas beyond recovery in the minds of recreationists, thereby exerting a long-term economic impact on the area. For the 22 000 ha Entiat fire in north-central Washington in 1970, Bakker observed a striking decline in recreation visits for 16 of 26 activity elements compared with the Wenatchee National Forest as a whole.^{4/} The maximum increase in visits was for viewing scenery (burned areas) (+10.7 percent), whereas guided-tour activity declined by 20.4 percent. He speculated that visual quality of the environment was a highly important factor in determining the value of a recreational experience for almost all activities. It appears, therefore, that longevity of effects will depend upon rate of revegetation of scars on the landscape. Siltation resulting from erosion of upland areas exerted a negative impact on opportunities for fishing for both native and anadromous fish. These recreational losses were offset to some degree by increased use by hunters as size of deer herds responded to increased forage resulting from secondary succession after the fire. The fire also opened the area and provided more visibility for hunters.

Extensive wildfires and the resultant smoke pall in interior Alaska's Mount McKinley National Park during the summer of 1969 did not affect total number

^{4/} Bakker, Pieter. 1975. Economic impacts of forest fires--the Entiat case. M.S. thesis. Univ. Wash., Seattle. 113 p.

of visitors but did reduce length of stay (Miller 1971). Miller observed increased use of the backcountry and of photography during this time, however, and speculated that it was because of lack of rain.

According to Connaughton (1972), fire has a greater impact on recreation than on any other forest use. Forest closure, because of high fire hazard or occurrence of fire, is one of the more obvious negative impacts for recreation. Bulldozer-constructed firelines were cited by McClelland (1975) as one of the more esthetically displeasing effects of fire-control activities. When the nutrient-rich surface soil is removed, these areas may remain barren for many years and present a sharp contrast to adjacent burned and unburned areas. Vegetative successional patterns were sufficiently retarded on such areas as to adversely affect esthetic quality. McClelland also indicated that salvage logging, once practiced in National Parks, is now deemed inappropriate.

In contrast to adverse effects of fire on recreation visitation, opportunities for some recreational activities are enhanced by fires and may even depend on periodic fire. McClelland (1975) pointed out that viewing lightning storms in Glacier National Park was an esthetically pleasing experience for visitors. Fire created natural vegetative diversity conducive to a variety of forest recreational uses. For example, western larch (Larix occidentalis Nutt.) and a variety of deciduous shrubs favored by fire provided a spectacular display of fall colors for visitors. Snags created by fire provided habitat for cavity nesters, and shrubs--such as huckleberry (Vaccinium spp.)--attracted grizzly and black bears for viewing and photographic opportunities for forest visitors that would have been more limited in an unburned forest.

In a 1978 review, Lyon and others concluded that larger wildlife prized as game increase after fire in response to modifications of habitat and successional patterns of vegetation. The expected result would be an increase in visitors to hunt and view the game. In contrast to favorable changes for wildlife, fire may temporarily displace or eliminate some species that depend upon later stages of plant community development; recreational opportunities to hunt, view, or photograph those species are then reduced or eliminated.

Huckleberry fields created by wildfire or slash burning after logging provide an excellent recreational opportunity for berrypickers in the Pacific Northwest (Connaughton 1972). Minore (1972) estimated that in a highly favorable year, one area in Washington State produced 1 047 liters of huckleberries per hectare. In addition to economic benefits, recreational benefits are enjoyed by berrypickers--in one Oregon area during the 1969 season, there were 163,000 visitor-days. Minore concludes that the huckleberry yield at Twin Buttes, Oreg., would equal or exceed the value of timber produced annually on most high-site forest land. Of additional interest is the fact that huckleberry fields appear to occupy sites that are marginal for timber production and conflict between fiber output and recreational enjoyment is minimized.

Stankey (1968) has studied knowledge and views of wildland fire among wilderness users. He found a fairly low level of understanding of the role of fire in forests, a majority of users favoring some level of fire suppression, and a substantial minority supporting a more natural role for fire in wilderness. He observed that few users found total suppression or no suppression acceptable.

The relationship of basic research to policy is not explicit in the revised Forest Service fire management policy of the Forest Service, U.S. Department of Agriculture (see footnote 1). Public reaction, however, was addressed in the U.S. Department of the Interior National Park Service policy (Kilgore and Briggs 1972). Kilgore and Briggs concluded that the "public seems ready to accept both the natural role of fire in the forest and our plans to restore fire to that role as nearly as possible and practicable."

Research aimed at assessing esthetic and recreational response to fire is in infant stages as reflected by the paucity of published work. Because of this, there does not yet appear to be any strong relationship between basic research and established policy. The public's attitude toward fire that evolves over the next several years will undoubtedly be a critical element in resolving conflicts associated with the use of prescribed fire. Stankey (1968) recommends education and involvement of the public, gradual changes in policy, and initiation of communication programs aimed at many different audiences.

OFFSITE ECONOMIC CONSEQUENCES OF FIRE

Offsite economic responses to forest fire and benefits resulting from prescribed fire are probably the least studied and most poorly characterized of any aspects of forest fire. One of the most frequently asked questions is, "What are the economic benefits in terms of protection and suppression cost savings in the use of prescribed fire to alleviate fuel buildups and prevent eventual costly conflagrations?" There is agreement in the fire management community that with effective protection and suppression efforts, forest fuels are building to the point that conflagrations are inevitable (Gale 1977). Zivnуска (1968) felt that the most obvious and important benefit of prescribed burning is the probable reduction of wildfires with their attendant high suppression costs and high potential for causing damage. For southern California, he concluded that magnitudes of benefits and costs associated with prescribed burning programs are largely unknown. In particular, he cited indirect costs as the most important to estimate because they are likely to outweigh direct costs. Probability of escape of a prescribed fire is an important indirect cost. Suppression and damages have involved several million dollars for documented individual prescribed fire escapes in the past. In addition, scheduling the fire, air pollution, losses of nutrients, and effects on watersheds are important indirect costs that must be considered. Smith (this volume) indicates that although research on quantification of fire damage has grown and mathematical modeling and simulation have been applied operationally, application of economic theory to reduce costs, enhance benefits, and optimize allocation of resources is lacking in fire planning.

Conflagrations are extremely costly as indicated by costs of \$5,019,522 to extinguish approximately 22 000 ha of fire in the Entiat Valley in north-central Washington in 1970 (see footnote 4). Seeding to control erosion, fertilization, cleaning streams, constructing trash racks and debris dams, and poisoning rodents boosted these costs by an additional \$392,132.

Kilgore and Briggs (1972) concluded that the revised fire management policy of the National Park Service has resulted in reduced costs of suppression. According to these authors, fires that should be allowed to run their courses are those that pose no threat to life, property, natural resource values, or where terrain is too rugged for suppression.

Bakker (see footnote 4) performed an in-depth analysis of the costs and benefits associated with the 22 000 ha Entiat Valley fire in 1970, in north-central Washington. This fire was unique in that it occurred in a narrow glacial valley where the local economy is strongly dependent on supplies of timber originating from the upper slopes, recreation based on sightseeing, summer homes, hunting and fishing, and fruit production. All these activities are dependent to some degree on water supplies originating within the valley. For continued economic health of the valley, it is obviously essential to maintain high quality water supplies from the upper slopes. Bakker considered both onsite and offsite effects in his analysis, including the following major elements:

Timber resource	- Loss of timber to owners - Change in land productivity - Loss of surrounding stands through secondary effects (wind)
Hydrologic resource	- Change in future fire danger - Property damage from landslides - Impact on various water users from changes in water temperature, sediment loads, water yield, and debris loads
Recreational resource	- Change in recreational value through esthetic degradation and destruction of improvements for recreation
Wildlife resource	- Change in hunting opportunities - Impact on some other recreational activities
Other resources	- Change in fishing opportunities - Impact on grazing permittees - Impact on property value from esthetic change - Change in educational value

Results of this analysis are shown in table 1. Bakker used 1970 dollars with a 10 percent discount rate. Optimistic assumptions were for low costs and high benefits, and pessimistic assumptions were just the reverse. According to his optimistic analysis, costs exceed benefits by nearly 10 times--and suppression costs comprise more than half the total costs. Under the pessimistic assumption, the gap was even wider (64 times). All costs except suppression and rehabilitation directly impacted people in the Entiat Valley through loss of revenue, property, and life. Wildlife was the only resource area that showed a benefit to the valley from fire. This was the result of an increase in big-game herds and attendant increases in hunter numbers. Bakker's results serve to reemphasize an urgent need to determine costs of prescribed fire or of alternate fuel hazard reduction means relative to benefits gained in reduction or elimination of fire presuppression and suppression costs.

In contrast to the adverse economic effects of wildfire on the Entiat Valley, when Bakker projected his results onto a regional scale (Chelan County, Wash.), he concluded that the region was better off for the fire because of increased Federal spending and resulting second-round effects. Therefore, effects on regional economies should also be considered in efforts to answer questions related to costs and benefits of prescribed burning.

No references were located that specifically addressed the issue of the relationship of economic offsite effects to fire frequency and intensity. Nor was any information found that related basic research on economic effects to fire management policy. Lack of information is probably a reflection of the early stage of research of this nature.

WATERSHED EFFECTS

Of all ecosystem components, water is perhaps the most sensitive to disturbance of vegetation and soils (Tiedemann and others 1979). It is not only a valuable resource product from forests and rangelands but also a transport mechanism for nutrients and sediment.

Sediment and turbidity are the most dramatic and important water quality responses associated with fire according to a recent review by Tiedemann and others (1979). They are also poorly documented aspects of fire-related watershed research, particularly with respect to origin and delivery rates. Sediment and turbidity result from overland flow of water and erosion of soil, channel scouring caused by increased stream discharge, dry ravel and creep accumulations in stream channels, and mass erosion. Sediment is generally considered to be coarser fractions (larger than clay-size fraction) of transported soil and geologic materials. Turbidity is in the colloidal size range which thus may remain suspended for considerable lengths of time.

In agricultural areas, sediment and turbidity plug irrigation lines and ruin pumping and water delivery systems. Sediment may also inundate crops. Sediment reduces the capacity and hence the life of storage reservoirs.

Lyon and others (1978) emphasized that sediment may reduce the area of anadromous fish spawning gravels or deposit fine materials that smother eggs and prevent emergence of fry. Populations of preferred food species of aquatic insects may also be reduced. One major effect of removal of streamside vegetation is reduction of available habitat for aquatic organisms.

Factors in the landscape that regulate erosion and are affected by fire have been summarized in reviews by Anderson and others (1976), Wells and others (1979), and Tiedemann and others (1979). Several of the hydrologic responses to fire are worthy of emphasis. Elimination of vegetative cover initially exposes the soil to greater impact from raindrops (DeByle and Packer 1972). Reduced infiltration rates and nonwettability problems associated with some soils (DeBano and others 1970) may cause increased overland flow and greater opportunity for soil erosion. In addition to exposing the soil, removing transpiring vegetative cover results in greater soil moisture storage (Klock and Helvey 1976a) and increased peak and total discharge (Rowe and others 1954, Sinclair and Hamilton 1955, Rich 1962, Pase and Ingebo 1965, Helvey 1973, Anderscn 1976, Campbell and others 1977). Greater stream channel exploration area and increased sediment production are the consequences of increased peak discharge. This problem may be aggravated by increased dry ravel and creep in areas with coarse soil materials and steep slopes (Krammes 1965, Mersereau and Dyrness 1972). This type of erosion problem is particularly acute if steep stream channel areas are burned as in the Entiat fire of eastern Washington described by Helvey (1973). This may create an epicycle whereby material deposited in or near the stream channel is flushed out by peak discharge in spring followed by more deposition during the dry summer months. This cycle may proceed until streambanks are stabilized by vegetation or a slope of about 30° is achieved.

Table 2 shows sediment production as a consequence of fire observed in several studies in the United States. It is apparent even from these limited data that wildfires create more sediment than prescribed fires. Overland flow (and potential erosion) is also more responsive to prescribed burning on steep slopes with finer textured soils than with coarser soils (Ursic 1969, 1970).

Wright and others (1976) studied the effect of slope steepness on turbidity after prescribed fire on dozed juniper lands in central Texas. On level slopes (1 to 4 percent), burning caused no change in turbidity compared with control watersheds; on moderate slopes (8 to 20 percent), turbidity more than doubled; and on steep slopes (37 to 61 percent), it increased by more than 10 times.

TABLE 1.--Impact of wildfire on a variety of resource outputs of values calculated at the 10-percent discount rate ^{1/}

Item	Costs		Benefits	
	High	Low	High	Low
----- Dollars -----				
Suppression	5,019,522	5,019,522		
Rehabilitation	392,132	392,132		
Timber resources	438,394	438,394		
Water resources	1,011,828	969,547	53,560	43,627
Recreation	818,432	818,432		
Wildlife	168,692	138,520	1,057,837	113,312
Fisheries	1,004,340	582,837		
Improvements	881,200	881,200		
Human (loss of life)	860,800	860,800		
	10,595,332	10,101,384	1,111,397	156,939
	<u>Optimistic assumptions</u>		<u>Pessimistic assumptions</u>	
Costs	10,101,384		10,595,332	
Benefits	1,111,397		156,939	
Total impacts	8,989,987		10,438,393	

^{1/} Adapted from Bakker, Pieter. 1975. Economic impacts of forest fires--the Entiat case. M.S. thesis. Univ. Wash., Seattle. 113 p.

TABLE 2.--Effects of fire on delivery of sediment

Reference	Habitat	Location	Treatment	Sediment transport (kg/ha/yr)	
				Pretreatment	Posttreatment
DeByle and Packer (1972)	Western larch Douglas-fir	Western Montana	Clearcut, broadcast burn	0	168
Glendenning and others (1961)	Arizona chaparral	Central Arizona	Wildfire	175	204 000
Wright and others (1976)	Oak-juniper on steep slopes	Texas	Broadcast burn	0.02	28
Biswell and Schultz (1957)	Ponderosa pine	California	Understory burn	0	0
Copley and others (1944)	Southern woodland	North Carolina	Prescribed burn	0	11 200
Meginnis (1935)	Oak-woodland	Mississippi	Harvest annual burning	45	740
Krammes (1960)	California chaparral	California	Wildfire	5 530	55 300
Campbell and others (1976)	Ponderosa pine	Northern Arizona	Wildfire	0-3	1-1 254
Anderson (1976)	Coastal forest	Western Oregon	Wildfire	522	2 955

In contrast to erosion observed after fire, in much of the United States initial and repeat prescribed burning during various seasons did not affect such movement in the Georgia Piedmont (Brender and Cooper 1968). Even 18 cm of rain in August from heavy downpours failed to initiate erosion. Similarly, Cushwa and others (1971) failed to detect soil movement in established gullies after prescribed burning in the South Carolina Piedmont. Most studies in the southeastern Coastal Plain conclude that periodic fire (wild or prescribed) has little impact on soil physical properties that affect infiltration rates or erosion (Suman and Halls 1955, Metz and others 1961, Moehring and others 1966, Ralston and Hatchell 1971, Stone 1971, Pritchett 1977). Large pore space may decrease and percolation may slow with short-interval (1- to 2-year) burns, but erosional consequences are negligible.

Stream Temperature

Water temperature has been shown to change markedly regardless of how shading is removed (Levno and Rothacher 1969, Anderson and others 1976).

Helvey and others (1976) measured increases in midsummer stream temperatures of up to 12.2°C after wildfire in steep mountain streams. Maximum water temperature reached 21°C. Significance of these values is not apparent until they are placed in perspective with the tolerances and requirements of aquatic organisms. The Environmental Protection Agency (1973) summarized temperature tolerances of several species of fish. Optimum and lethal temperatures for a selected variety of these organisms are presented in table 3.

Maximum temperature observed by Helvey and others (1976) is beyond optimum and maximum weekly average temperature for preserving adequate rates of growth of sockeye salmon, brook trout, and brown trout, but within limits given for bluegills and smallmouth bass. The upper incipient lethal temperature was not exceeded for any of the five species.

TABLE 3.--Temperature (°C) tolerances of various fishes^{1/}

Species	Optimum temperature	Ultimate upper incipient lethal temperature	Maximum weekly average temperature
Bluegills (<u>Lepomis macrochirus</u>)	22	34	26
Smallmouth bass (<u>Micropterus dolomieu</u>)	26	35	30
Sockeye salmon (<u>Oncorhynchus nerka</u>)	15	25	18
Brook trout (<u>Salvelinus fontinalis</u>)	15	26	18
Brown trout (<u>Salmo trutta</u>)	12	24	16

^{1/}From Environmental Protection Agency (1973).

Plant communities accumulate and cycle substantial quantities of nutrients in their role as the biological continuum linking soil, water, and atmosphere. Nutrients are cycled in an orderly and predictable manner unless some disturbance causes a change in the form or distribution of nutrients. Fire exerts profound effects on the nutrient status of plant communities manifested by a rapid mineralization and dispersion of plant nutrients from an intrabiotic to an extrabiotic state. Part of the plant- and litter-incorporated N, phosphorus (P), K, Ca, Mg, copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) are oxidized or volatilized and may be evacuated from the system (Allen 1964, DeBell and Ralston 1970, Evans and Allen 1971, Grier 1975). Metallic nutrient elements (such as Ca, Mg, and K) are converted to oxides and deposited as ash on the soil surface. These oxides are low in solubility until they react with CO_2 and H_2O of the atmosphere and are converted to bicarbonate salts. In this form, they are substantially more soluble and vulnerable to loss via surface runoff and leaching than when incorporated in plant tissue and litter. Reduced plant cover after fire increases susceptibility of nutrients to erosion and severed soil-plant cycling mechanisms reduce opportunity for nutrient uptake.

Above-normal movement of nutrients to streams via surface erosion and leaching has a potential for impairing quality of surface water for municipal purposes and for causing eutrophication of aquatic habitats.

Of the nitrogen compounds found in surface waters, $\text{NO}_3\text{-N}$ has been emphasized because it is one of the most mobile ions in soil-water systems, and is one of two forms of N utilized by plants. EPA (Environmental Protection Agency 1973) has recommended a standard of 10-mg/liter maximum of N as nitrate.

Nitrate-N concentrations are normally at very low levels in streams from undisturbed areas, ranging from less than 0.01 mg/liter (Fredriksen 1971, Tiedemann 1973, Helvey and others 1976) to 1.2 mg/liter (Brown and others 1973).

Striking increases in $\text{NO}_3\text{-N}$ concentrations have been observed in several studies after wildfire and prescribed fire (Fredriksen 1971, Brown and others 1973, Tiedemann 1973, Snyder and others 1975, Kimmins and Feller 1976, Tiedemann and others 1978). Maximum observed values, however, have been within limits proposed by the Environmental Protection Agency (< 10 mg/liter). In contrast, some researchers have detected no change in surface water levels of $\text{NO}_3\text{-N}$ after fire (Lotspeich and others 1970, Wright 1976, McColl and Grigal 1977).

Interest in P as a pollutant has been spurred by knowledge of its eutrophying effects in areas where large quantities emanate from sewage treatment plants as a result of high phosphate detergents.

Phosphorus in soil solution and in stream waters and lakes is present mainly in two forms--orthophosphate (inorganic) and organic phosphate.

Several studies of watersheds (Lotspeich and others 1970, Fredriksen 1971, McColl and Grigal 1975, Kimmins and Feller 1976, Brown and others 1973, Longstreth and Patten 1975) have shown that fire does not affect stream water P. In contrast to results of these studies, Tiedemann and others (1978) found that P levels in streams from burned watersheds were two to three times greater than in a stream from an unburned watershed. Also, Lotspeich (1972) found a temporary increase in P in a stream in Alaska as the result of use of 228 000 liters of fire retardant.

After wildfire in the Boundary Waters Canoe Area of northeastern Minnesota, Wright (1976) measured an increase of 38 percent in P-loading of one lake. He concludes, however, that this was within limits of natural variation and was not a significant impact on the lake.

Mass Erosion and Debris Flood Consequences of Fire

Mass erosion, the downslope movement of a portion of the landscape under direct application of gravitational forces, has been documented as an important postfire phenomenon in southern California, the Pacific Northwest, and the Intermountain West^{5/} (Croft and Adams 1950, Sinclair and Hamilton 1955, Swanston 1971, Rice 1974, Klock and Helvey 1976b). This type of erosion has caused loss of life, destruction of roads and buildings, loss of aquatic habitats, and inundation of agricultural areas. For example, in Los Angeles County, the Montrose Flood of 1934, following a 2 000 ha fire, killed 34 people and caused \$5 million in damage (Office of Emergency Preparedness 1972). Debris flows in north-central Washington in 1972, after wildfire in 1970, killed four people and destroyed several residences (Klock and Helvey 1976b). Several thousand cubic meters of debris were estimated to have flowed from one watershed. Jensen and Cole (see footnote 5) reported that an intense fire on 364 ha of steep slopes adjacent to the south fork of the Salmon River in Idaho caused mass landslide erosion that delivered 34 400 m³ of debris directly to the river.

Causative mechanisms and processes of mass erosion are complex and generally have not been studied. The principal causes of mass erosion in most areas are elimination of stability provided by roots of vegetation and high soil-pore water pressures resulting from removal of transpiration draft (Swanston 1971, Klock in press). Mass movement either develops or is accelerated during periods of abnormally high rainfall and is closely related to peak flows generated by such storms (Swanston 1971). In addition, soil nonwettability has been identified as an important contributing factor in debris flows or floods in California (DeBano 1970, DeBano and others 1977).

Mass erosion events in California chaparral most commonly occur as debris floods or debris flows. The debris bulking ratio (ratio of volume of debris to volume of water) increases from 2 to 15 times after fire (Rowe and others 1954, Sinclair and Hamilton 1955, Rice 1974). Increased debris bulking ratio, coupled with increased storm runoff, is the principal cause of disastrous debris floods that occur in southern California.

In the transverse ranges of California, soil slips are abundant on brush-covered watersheds but not on recently burned watersheds where rilling is a more pronounced manifestation of erosion (Rice 1974). This is an example in which fire exclusion may actually promote mass soil movement.

Aquatic Habitat Responses

We are accumulating an extensive data base on effects of fire on sediment, turbidity, nutrients, and stream water temperature and chemistry, but studies on attendant responses at the stream or lake level are meager. Lotspeich and others (1970) studied stream macroinvertebrate responses to wildfire in Alaska. They concluded that changes in chemical makeup of the water were below the magnitude necessary to exert an impact on the aquatic organisms they studied.

^{5/}Jensen, F., and G. F. Cole. 1965. South Fork of the Salmon River storm and flood report. Unpubl. rep. on file at Intermountain Forest and Range Experiment Station, Boise, Idaho.

Hoffman and Ferreira (1976) examined periphytic algae above and below burned sites and found essentially no difference in the similarity index, indicating that water quality changes did not exert any effect on growth of algae. Results were the same for benthic macroinvertebrates. Wood^{6/} was unable to demonstrate any significant changes in species diversity or numbers of aquatic macroinvertebrates when streams were exposed by clearcutting and slash burning.

Relationship to Fire Frequency and Intensity

Effects on watersheds are somewhat unique in comparison with other offsite effects considered in this paper; they can be more closely related to fire size, relative intensity, and disturbance of critical areas, such as riparian habitat. Much needs to be accomplished in relating offsite effects to frequency of fires. Most of our information on hydrologic response to frequent fires comes from the southeastern United States. There is little such information for the West.

Role of Basic Research in Policy Development

Basic research has played a crucial role in the development of water quality standards which apply to all activities on the landscape, including prescribed fires. In development of the 1972 water quality criteria, the Environmental Protection Agency (1973) attempted to characterize water quality limits for the full range of uses of various waters and for requirements and tolerances of aquatic organisms.

Although not explicit in the laws themselves, there is little doubt that basic research played an important role in the development of P.L. 92-500, the 1972 amendments to the Federal Water Pollution Control Act (U.S. Laws, Statutes, etc. 1972), and P.L. 94-588, the National Forest Management Act (U.S. Laws, Statutes, etc. 1976). Section 208 of P.L. 92-500 specifically mandates identification and control of, to the extent feasible, nonpoint source pollutants resulting from silvicultural activities. P.L. 94-588 specifies that land management plans ensure protection of soil and water resources.

Some States mandate protection of the riparian zone during prescribed burning operations. For example, in the Appalachians, prescribed burning is prohibited within watercourse buffer strips.^{7/} The width of a defined protection strip varies from 9 to 88 m depending on predicted erosion hazard and slope steepness.

In California, broadcast burning is prohibited within stream and lake protection zones^{8/} --a strip of soil and vegetation along both sides of a stream or around a lake to a distance of 30 m from where riparian vegetation is permanently established if the stream or lake is used by trout or anadromous fish. A distance of 15 m is established for the protection of other streams and lakes.

^{6/}Wood, John R. 1977. The aquatic insects of Rainy Creek with special reference to caddisflies (Trichoptera). M.S. thesis. Cent. Wash. Univ., Ellensburg. 71 p.

^{7/}Personal communication from Monte E. Seehorn, Regional Fisheries Biologist, USDA Forest Service, Alanta, Ga.

^{8/}Amended Forest Practices Rules, adopted by State Board of Forestry, pursuant to Article 4, Division 4, Chapter 8, Public Resources Code, California Administrative Code Title 14, Division 2, Chapter 2, effective August 25, 1975.

SUMMARY

I've presented an overview of factors considered to be important offsite consequences of forest fire. It is evident that air quality aspects of smoke and effects on watersheds are the areas most adequately covered by research.

For most of the elements, it was difficult to relate fire frequency and intensity to a specific effect. This is reasonable, however, since we are just now entering an era where prescribed burning may become commonplace. Much of our previous information was the result of study of aftermath of wildfire. In many cases, little prefire information was available for a truly accurate assessment of effects.

DeBruin and others (1980), in reviewing the evolution of wildland fire policy in the United States, concluded that basic science and scientists have played a fundamental role in establishment and revision of the wildland fire management policy in the United States. Fire is now recognized as a major natural recycling agent for plant elements and for maintaining a natural equilibrium between dead and live components of forests.

They indicate, however, that science has been only one of the elements in fire policy evolution and that such a major social change also relies on the ensemble of cultural institutions, beliefs, practices, and mores.

For most of the offsite considerations, it was also difficult to make positive connections between basic research and development of policy. Much of this difficulty likely stems from the fact that most of the policy statements related to fire are not explicit about the rationale for their evolution in terms of the role of basic research. This does not mean that research results were not used for formulation of policy--only that they are not included in the final policy document.

As I reviewed material for this paper, it became increasingly evident that we must fine-tune our skills in evaluating, as accurately as possible, the full range of offsite consequences of fire if we are to establish rational plans to utilize fire for wildland management that will avoid conflict between fire and people.

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FIRE AND PUBLIC POLICY

David W. Dahl, Steve Pyne, Ernest V. Anderson, Trenton Crow ^{1/}
Aviation and Fire Management
USDA Forest Service
Washington, D.C.

ABSTRACT

The fire management policy of the USDA Forest Service was revised in 1978 to permit cost-effective fire suppression tactics to be employed. Further, fire management activities are directed to meet land management objectives. This paper examines some of the factors involved with changing fire management policy. Emphasis is on the influence of the Industrial Revolution, European culture, 1910 fires, mores of early foresters in America, scientific technology, philosophy, and the post-1910 period including the influence of the Civilian Conservation Corps. Public policy is presented as a dynamic political manifestation of interactions of these factors.

KEYWORDS: fire management, fire policy, public policy

PROLOGUE

In 1978, the USDA Forest Service changed its policy, established in 1935, for managing fire on National Forest land. For over 40 years Forest Service employees were guided by a policy which stated:

Fire suppression will be fast, energetic, thorough, and conducted with a high degree of regard for personal safety. . . .

When first attack fails...organize and activate sufficient strength to control every fire within the first work period. If the fire is not controlled in the first work period, the attack each succeeding day will be planned and executed to obtain control before 10 o'clock the next morning. (Emphasis added.)

^{1/} This paper was presented by Henry W. DeBruin, Director of Aviation and Fire Management, USDA Forest Service, Washington, D.C.

Each fire was to be controlled regardless of burning conditions or natural resource management objectives. In order to meet this policy, large expenditures were made on fires to minimize acreage burned.

Now, Forest Service land managers are being directed: ". . . if a fire escapes initial attack, an escaped fire situation analysis must be made. This situation analysis will include cost-effective fire suppression alternatives and will serve as the basis for deciding which alternative to use." In addition the policy specifies that:

1. Fire management planning be totally integrated into Forest Service land management planning process.
2. In areas where natural resource conditions, such as wildlife habitat, can be improved by prescription fire and where plans have been approved for this purpose, the fire suppression action may be modified to meet these resource management objectives.
3. Land managers are to make more use of prescription fire to protect, maintain, and enhance the natural resource values and esthetics within approved areas on the National Forest.
4. Fire protection and use programs will be planned to be cost effective and will provide protection for life and property, public safety, values, and natural resource management programs.

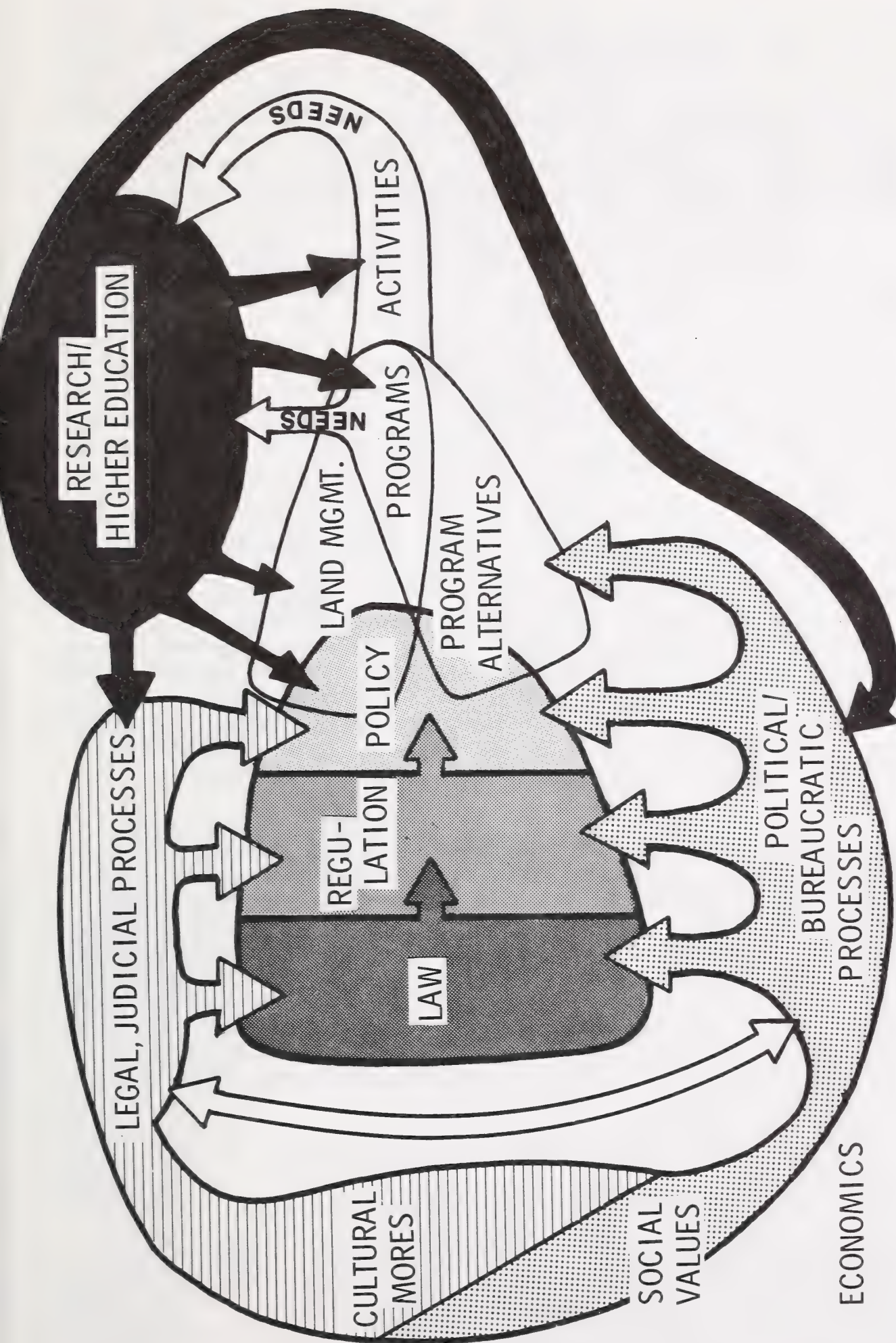
The purpose of this paper is to examine components which contribute to development of public policy relating to fire. This paper will concentrate on the National Forest System's policy. The principles developed are applicable to most public agencies in the United States or other free countries throughout the world.

INTRODUCTION

The 1978 "managed" fire policy did not develop as a linear succession of policy decisions. It was the result of a complex network of forces (fig. 1). Philosophy, scientific technology, cultural mores, and historical events were some of the forces involved. These driving forces became manifested in the political process. This political process results in laws and regulations often interpreted by the judicial process; which are again influenced by cultural mores and social values of a public.

The influence of individuals or small groups of people within public agencies often results in increasing or decreasing rate of policy change. This influence is also important as regulations are translated to policy and to some degree as laws are interpreted into regulations. These influences are further affected by cultural mores, social values, and the scientific backgrounds of influential individuals. In turn, the political process affects research and development of scientific technology through program development and budgeting.

A complete understanding of the development of public policy relating to fire cannot be gained by studying history of fire organizations only. To completely understand we must look at events, incidents, concerns, and assumptions far removed from decisions about how to use or exclude fire from the environment. We must broaden our study to include many events, cultural mores, laws and regulations, scientific technologies, and philosophies which affect policy and view them in their role of impacting public policy toward fire.



FIRE MANAGEMENT POLICY INFLUENCES & RELATIONSHIPS

Figure 1.--Fire management policy influences and relationships.

DOMESTICATION OF FIRE

Fire policy is not something new. We feel that ever since fire was first domesticated, societies have devised practices and public policies to provide for protection from unwanted fires as well as to prescribe for its use. The Old Testament established policies against setting wildfires or allowing fires to escape and damage property of others.

Social values and economic demands have traditionally played important roles in "policy" development. There is evidence that fire was used early to protect the faces of naval stores trees in the southeastern United States. The first European settlers in the United States (Jamestown, Va.) were sponsored primarily because costs of using coal for glass production in England were higher than costs of using American forests. European demand for glass increased demands on American forests. With these strong economic demands for timber, English colonies in the New World found it necessary to restrict the use of fire to specific seasons, places, and activities, and to provide restitution to those damaged by escaped fires.

As societies evolved, new situations called for new considerations of fire problems. For example, fires which were suitable for a hunting and gathering society were not appropriate for one based on agriculture. Conflicts like this occurred in California where Indians used fires for the harvesting of insects, nuts, and small mammals. This use of fire conflicted with the Spanish pastoral economy. In 1775, the situation became so critical that authorities in Santa Barbara prohibited the setting of brush and grass fires and directed troops from the Presidio to take action to control these fires. A century later the use of fire for improving forage conflicted with industrial demands for timber. When timber attained a value for industrial purposes, protection became important and controversy arose. Again in California--on new parklands--Federal troops were directed to prevent fires from starting and to control wildfires.

The development of public policy in the United States is both complex and dynamic. On one hand, it involves the displacement of one cultural environment by another. European colonists, assisted by plagues among American Indian populations, exploded into population and cultural vacuums. Traditional constraints and pressures vanished; particularly for settlers from Northern Europe where fires were infrequent, newcomers did not know how to behave toward their new natural environment. For this reason, prolonged experimentation with various policies toward wildland and rural fire was predictable. On the other hand, people were experiencing a folk migration of unprecedented proportions and were undergoing rapid economic, social, and intellectual revolutions, and were therefore themselves altering the cultural environment and natural landscape quite radically.

FORCES DEVELOPING PUBLIC POLICY IN THE U.S.

The policy of any public agency today, although fixed at any point in time, is temporal as in total the forces or components affecting it are dynamic. Many of these forces are tightly interwoven and some are relatively stable. Others are changing as social, cultural, economic, and political processes interplay in their effect on policy. Let's examine some of these forces more closely.

Industrial Revolution

As industrialism came to North America, it increased the risk of ignition. (The locomotive and friction match, for example, both arrived in 1837.) It increased the demand for natural resources, especially forest products and fossil fuels. This altered fuel complexes and caused many of the massive fires recorded in the late 19th and early 20th centuries. But, the industrial revolution also brought promise of

better control over destructive fires. It was felt that the introduction of science and engineering into politics and industry could rationalize processes and reduce waste. As a developing nation, the United States looked to successful industrial societies for guidance; U.S. students flocked to German, French, and English universities. The process of technology transfer was not always accurate.

In conceptualizing conservation, early proponents believed that professional bodies of scientists and engineers operating out of government bureaus could reestablish social and environmental equilibria upset by the industrial revolution. In many cases, these concepts and related technology transfer worked admirably. In other cases these ideas led to serious problems.

European Culture

European foresters were not always familiar with fire as an environmental factor. Lightning fires were relatively infrequent in Europe. Therefore, European explorers often equated the presence of wildland fire with the presence of people. Moreover, with careful gleaning of fuel from forest floors of well-managed forests, well-defined ownerships and responsibilities, and with prevention practices reinforced by centuries of folk tradition, fire of any sort was relatively rare in European forests. A fire of 50 acres might be discussed for years. In the United States conditions were such that fires of thousands of acres could be expected every few years, often with little or no thought given to them. However, in the United States, the industrial revolution combined with increasing population to create conditions for different public policies toward fire. The development of fire policy in the United States shows how these two forces have interacted with each other and with other factors in economics, social values, cultural mores, political forces, laws, regulations, scientific technology, and philosophy. These factors are not mutually exclusive as graphically illustrated in figure 1, but are interdependent.

1910 Fires as a Catalyst

Policies of excluding and suppressing fire existed prior to 1910, but were not always effectively applied. The Federal Government became involved in 1886, when the Army took over administration of Yellowstone National Park and promptly went to work fighting 60 fires that first summer. The first State lands to receive protection came a year earlier with the establishment of Adirondack State Park in New York. After the 1902 Yacolt Fire in Washington, a number of private protective associations emerged in the Northwest. Following the Forest Management Act of 1897, the Government Land Office attempted fire protection on forest reserves. The attempts were accelerated after the reserves were transferred to the Forest Service in 1905. The "Use Book" which guided administrative management made fire prevention and suppression a primary responsibility of Forest Officers. Fire was an emergency that took precedence over nearly every other assignment. Deficit spending to finance forest fire fighting became possible and was a generally accepted practice after 1908. But it took the great fires of 1910 to catalyze a major endeavor. The devastating fires of 1910 provided the basis for a strong national policy and the administrative apparatus which mobilized wildland fire protection into an effective organization.

The 1910 fires were a complex of fires burning in Idaho and western Montana which blew up under hurricane-like winds on August 23 and 24. The fires roared over farms, towns (such as Wallace, Idaho), and some 3¼ million acres of forest; 85 firefighters died in the blaze. The fire itself was not enough to cause changes in policy that followed. After all, the 1898 fire which burned 3-million acres in North Carolina did not even make the front pages of the Raleigh News and Observer. It required a context that made the fire a significant factor in altering policy. That context was conservation.

In 1910 concern over conservation was growing. Charles Van Hise published his Conservation of the Natural Resources of the United States--the first scientific

inventory of the country's natural resources, and the first textbook on conservation. Gifford Pinchot wrote his Fight for Conservation. The Governor's Conference on Conservation was 2 years old in 1910 as was the Inland Waterways Commission. Teddy Roosevelt had, by proclamation, doubled the National Forest System the year before.

At the time of the 1910 fires, if anyone were to have suggested that fire in the woods might be useful, or even essential, or if someone were to have urged that it was necessary to discriminate between natural and human-caused fires, they would have been severely criticized by professional foresters and ardent conservationists. Such criticism occurred between 1910 and 1924, in the famous California "light burning" controversy. A decision against light burning was made. This decision was understandable in this particular era.

Attitudes of Early Foresters in America

Many of the cultural mores concerning fire policy which exist today began with the 1910 fires. For American foresters the spectacle of a 3-million-acre fire was a source of acute embarrassment. Professional forestry was still in its infancy; most of its American representatives had, in fact, been trained in Europe. Foresters conceived of themselves as scientific engineers, like mining, mechanical, chemical, and electrical engineers who began to appear at the same time. The dominant intellectual thrust for conservation had come from such a brotherhood of applied scientists. Yet it was obvious that before the principles of professional foresters could be tested, forests had to be protected.

Annual uncontrolled fires made a mockery of the professional pretensions of foresters to carefully manage American forests. These fires were a sobering problem. At one point, an entire issue of American Forests was devoted to the 1910 holocaust.

Foresters, in addition, sought to professionalize forestry and make it synonymous with the drive for conservation: to demean one was to damage the other. If foresters were shown to have improperly transferred European experience to the New World with the fire issue, then the entire conservation program might collapse. In British colonies like India and Burma, attempts at the elimination of fire were shown to be questionable, and practices changed; in young developing energetic countries still enthusiastic over their independence from Europe, modifications were more difficult to make. Proposals to lightly burn forests were uniformly dismissed by the dedicated, professionals as "Paiute Forestry"--relic practices from a primitive stage of human culture which the United States as an industrial nation had evolved beyond.

Scientific Technology

Such attitudes had considerable support from the biological and social sciences. It is difficult today to appreciate how thoroughly evolutionism saturated all fields of thought in the late 19th and early 20th centuries. Nearly every discipline organized its subject according to an evolutionary scheme.

In 1910, wildland fire was given a similar theoretical foundation with the publication of Frederic Clements' "History of Fire in the Lodgepole Pine." Through further studies Clements articulated the theory of biological succession, which pictured biological communities as passing through a series of stages in their life cycle, beginning with a simple pioneer stage and concluding with a self-maintaining climax stage. If the cycle were interrupted--as with a major fire--the entire process would begin anew.

Clements' theory was indicative of the thought of the day: his biological landscape behaved exactly like the geological landscapes of William Morris Davis and the social landscapes portrayed by Frederick Jackson Turner on the American Frontier.

So, although communities could adapt to fire, fire was undesirable: it retarded the progress to a climax state. It was openly admitted, also, that nature's economy--like that of recent industrial nations--was wasteful and corrupt. Disorder and extravagance were visible everywhere. But proper scientific engineering could reduce this waste. Rivers could be tamed for useful energy; predators could be removed to allow useful game to multiply; and forest fires could be eliminated. In removing such waste, scientific engineering would actually assist nature as well as man. Thus, fire suppression received justification from a theoretical science developed in America as well as the experimentation of forest engineering in Europe.

Philosophy

At the time of the 1910 fires, the American philosopher William James published his famous essay, "On the Moral Equivalent of War." Growing out of the same atmosphere of Darwinism that led to the evolutionism of Clements' forest succession, James maintained that the struggle for existence was universally displayed in the natural and social worlds. He admitted, too, the values of the military spirit, and its inevitability, but sought to redirect it to more moral purposes. James urged, in particular, a national recruitment of youths to begin a war on the forces of nature. Such a proposal would be likely to animate conservation in general, and firefighting in particular. The stories of heroism that poured out from the 1910 fire, such as the exploits of Halart Pulaski, gave credence to the analogy. By the time of the New Deal and Civilian Conservation Corps (CCC), the parallel was obvious. But the atmosphere which stirred James also gave to firefighting a moral energy without which its success would be impossible to understand. The analogy between firefighting and warfare acquired an intellectual as well as emotional appeal, and it is perhaps no accident that the flow of enthusiasm for fire protection has been largely coincidental with that for the military. Thus, firefighting enjoyed great energy and purpose after World War II, but experienced only doubt, indecisiveness, and even hostility about the time of the Vietnam conflict.

The 1910 fire did not begin a national policy toward forest fires. One already existed. But it catalyzed prevalent trends and sentiments to such a degree that it reinforced the idea such that modern forest fire protection really began in the wake of the 1910 fire. However, it took the implementation of laws to instigate modern policy. After the Weeks Act in 1911 and the Clarke-McNary Act of 1924, fire protection had an administrative structure. The execution of regulations and application of policy was strengthened, and modern fire suppression in the United States was born.

Post-1910 Period

After 1910, an effective policy dealing with wildfire passed through four major phases. The first was the endeavor to give fire protection an administrative focus and to institutionalize it into laws and regulations. This was the concern through the 1920's. The second was to give fire protection an adequate physical plant and manpower. This was accomplished during the 1930's. The third was an appeal to technology, to develop or transfer from military surplus an arsenal of mechanized hardware. This occurred after World War II, again demonstrating the coincidental nature of war and fire suppression. Fourth, and finally, in the 1970's, the effort to control wildfire through widespread fuels management became popular. None of these undertakings were exclusive of the others, of course, and every attempt to establish a policy that would limit wildfire witnessed a simultaneous debate of how and even whether to reintroduce fire into the environment.

Actions emanating from changes in public policy did not receive application at the same time in all geographic areas. For example, early conversion of lands to agriculture

As late as 1931, efforts to develop wildland fire prevention and suppression programs by the State of Missouri met significant public resistance. Economics were probably not at the heart of this resistance. Social values and cultural mores were being questioned by the development of wildland fire protection programs.

In 1935, the Forest Service published its aggressive stance of initial attack known as the 10 a.m. Policy. In an attempt to simplify objectives of fire protection, it thereby motivated national fire organizations and biased the direction of fire control for decades.

In its day, the 10 a.m. policy made sense to many. The Forest Service had, for several years prior to 1935, been engaged in a debate about what level of fire protection to extend to "low value backcountry." The entire fire program came under serious review. Confusion was widespread. Particularly in remote areas ignited by lightning strikes, fires were left to burn. But the early 1930's were drought years across the United States. The Dust Bowl was but one indication. Major fires occurred in Virginia's Dismal Swamp, in Oregon's Tillamook Region, in Matilija Canyon of California, and in the Northern Rockies. In the summer of 1934, two major fires burned on the Selway National Forest. Like the great fires of 1910, these fires were the stimulation that provoked a majority of Regional Foresters in April of 1935 to agree on the aggressive new policy known as the 10 a.m. policy. Yet in this instance, as in 1910, the fires alone were not responsible. There were many precedents for the 10 a.m. policy within the Forest Service; "control in the first work period" had, for example, been incorporated in the Fire Code for the Eastern Forest District in 1926. The 1933 Copeland report outlined an ambitious program for fire protection. But, the 10 a.m. policy may have been unworkable without the presence of the Civilian Conservation Corps and Federal Emergency Conservation money. The physical necessities for fire protection--the roads, towers, guard stations, telephone lines--were available overnight instead of over decades as it might have been without these added capabilities. An organized source of labor appeared in quantities exceeding normal expectations. Only a few months after its creation, the CCC sent 500 enrollees to the Tillamook fire in Oregon. The experience with CCC led to an experimental 40-man crew which was the pattern for organized fire crews developed after the war. The CCC not only made fire protection possible on a scale previously unimaginable, it practically required it: fire protection improvements were major opportunities for the massive manpower suddenly released. Without the CCC, the debate about roads into backcountry was academic: there would have been no money. With CCC, roads became a reality. It is not likely that the 10 a.m. policy would have evolved without other forces that premitted its application. The policy needed the influence of the CCC.

One reason that the 10 a.m. policy didn't end after World War II was the way the war itself ended. More than in any previous war, World War II saw the use of fires as an offensive weapon. The fire bombings of Dresden, Hamburg, and Tokyo, and the explosion of the atomic bomb made fires a likely prospect of any future conflict. With lengthening of the Cold War, and development of thermonuclear weapons, wildland fire agencies became paramilitary extensions of Civil Defense--responsible for rural fire defense, research into the phenomena of mass fire, and the investigation of fires in both urban and wildland environments. During the Vietnam War, attempts were made to strip the forests through the use of "Agent Orange" and then the introduction of fire. Although these actions were not entirely successful, fire was a part of military tactics.

In 1954, the Forest Service was charged with rural and wildland fire defense, and in 1972, was given responsibility to administer funds for the Rural Community Fire Program. As military surplus equipment became available, it was possible to employ hard technology against the war on fire. Furthermore, there occurred a series of tragic fires involving loss of crews--Mann Gulch in 1949; Rattlesnake in 1953; Inaja in 1956--and two fires that involved rural communities as well as wildlands--the Texas

and Maine fires of 1947. In such circumstances, a "weakening" or even a readjustment of a strong defense strategy against fire was unlikely.

In spite of strong, aggressive stances toward fire suppression, the dynamic nature of policy still exists and the past decade has again seen national fire policies changing. In 1968, the National Park Service, following recommendations laid down by the Leopold report, allowed for the use of lightning-caused fire and prescribed burning in the management of natural lands. After 10 years of Service-wide experimentation in fire management programs, a national handbook on the subject was prepared. Although other Federal agencies have originated and/or reinforced fire suppression and use policies recently, changes continue to occur. In 1971, the USDA Forest Service amended the 1935 policy to allow for exceptions for certain areas, provided they had a nationally approved fire management plan. In 1978, the revised policy was established as discussed in the prologue.

Impact of Science

We feel that these changes involve a new perception of fire's function in wildland ecosystems. This view may have originated because of basic changes in theoretical foundations of the life sciences. The evolutionary thought which dominated nearly all dimensions of natural history from the early 19th century to the mid-20th century has been altered by concepts derived from cybernetics and systems theory. Today, it is generally accepted that ecosystem dynamics function in a steady state, revolving around rough norms dependent on energy transfers to recycle important nutrients and materials. Rather than an interrupting force in the evolutionary succession of communities, fire is viewed as an agent in recycling or maintaining nature's ongoing equilibrium. Scientists studying before and after pictures of forest fires in the 1920's would have pointed out lack of understory growth and reproduction. The same photos today would be viewed with a different perspective that would stress the dynamic aspects of the ecosystem.

In 1866, Ernst Haeckel coined the term forest "ecology" and inaugurated it as a subject. In 1916, R. H. Boerker reviewed the subject by publishing "A Historical Study of Forest Ecology" of over 100 pages. Just as evolution had once changed the meaning of "ecology," so the impact of information theory, cybernetics, and systems theory changed it again. As a result of these changes, fire in the environment was viewed with new perspectives. Changes in fire protection policy and practices reflect this new perception. Thus, the role of basic science has been fundamental in both establishing and revising wildland fire policy of the United States. These advances in science have played a dramatic role in policy change.

However, scientific theory does not begin to influence policy until it is generally known and accepted by practitioners. Therefore, technology transfer is a key element in measuring the impact of research results on policy and practice.

This fundamental role of science and scientists, however, should not lead to the conclusion that science has been a prime influence in affecting official public policy. There must be justification in theory as well. Science is a cultural product. And major theoretical revisions are rare without concomitant societal changes. A major social commitment represents a consolidation of cultural institutions, beliefs, practices, and mores.

Behind any changes of scientific theory is the influence of cumulative information. Major shifts in the sciences are understandable. Some 40 to 50 years passed between the first clamoring for forest conservation and the 1910 fire; another 40 to 50 years before the contemporary interpretation of ecology was popularized. Between Haeckel's invention of the term "ecology" and Boerker's review of it 50 years later, there had been two to three periods of information doubling. Between Clements' theory and contemporary

thought, another two to three periods of knowledge doubling have passed. Since the 1910 fire, our biological information in general has doubled four to five times, an increase of 16 to 32 times the information available when a vigorous fire program was seriously undertaken. If this pattern continues, the information base on which contemporary policies are founded will double several times more before the 20th century ends. Current theory is bound to be modified. Yet, this explosion of scientific information is only one aspect of cultural change and environmental modification, and both of these no doubt will strongly influence future fire policies.

CONCLUSION

In 1978, the Forest Service revised policy regarding fire on National Forest land. This fire policy is different from other policies the Forest Service has had and the policy other public agencies still have. It may differ from future policies. The forces that form current policy are varied and complex. Cultural mores and social values of the public combine with economics to form an integral part of the process. These are reflected administratively in laws and regulations generated by the political process. Events, such as the 1910 fires, are often catalysts that cause these forces to crystalize into new policies. The new policies result in funds budgeted toward program developments. These political actions flow through land management agencies and often initiate new research programs. The output of scientific technology developed from this research flows back through the system and influences preceding components.

Obviously public policy relating to fire is not and cannot be static. In the future, as today, policy decisions will be made by the interactions of all the component values of the day, assuring the continuous development and implementation of future policies.

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SLASH AND BURN AGRICULTURE IN NORTHEASTERN INDIA

P. S. Ramakrishnan, O. P. Toky, B. K. Misra, and K. G. Saxena

Department of Botany, School of Life Sciences
North-Eastern Hill University, Shillong, India

ABSTRACT

The tribal population of the Northeastern Hill tracts of India practices shifting agriculture which involves "slash and burn" followed by mixed cropping, a process which is locally called "Jhum" which is described in detail. Due to shortening of the Jhum cycle from about 20 to 30 years to about 4 to 5 years because of high population densities and reduced acreage, rapid deterioration of the local environment has ensued. This change is related to a number of factors such as intense soil erosion and rapid loss of fertility due to runoff and percolation losses; often irreversible loss of forest cover and consequent changes in microclimate of the area; rapid spread of exotic weeds with succession arrested indefinitely at the pioneer stage; and rapid depletion of wild germ plasm with a large number of species on the endangered list. These changes in the local environment could have repercussions in the northern plains of India in the form of floods, deposition of silt, or even major changes in the climate of the subcontinent itself. Since Jhum is a way of life of the tribal people of this region, it is suggested that it should be restricted and modified to minimize damage to the environment. It may be desirable to restrict cereal cultivation to a minimum and encourage horticulture and other perennial crops which may cause less damage to the environment from a long-term point of view.

KEYWORDS: slash and burn, shifting agriculture, agro-ecosystem, forest ecosystem, succession, water cycle, nutrient cycle, environmental damage, erosion, Jhum

INTRODUCTION

The tribal population of the Northeastern Hill tracts of India practice shifting agriculture which involves "slash and burn" followed by mixed cropping. This process is locally called "Jhum." After cultivation for some time, the land is left fallow, again to be cultivated in a few years. This cycle was previously spread over 20 to 30 years; however, under present conditions of higher population densities and reduced

acreage, the cycle may be as short as 4 to 5 years. Shorter cycles adversely affect the quality of the environment both in terms of soil fertility and vegetational cover. This paper is a preliminary report on a long-term study of the impact of slash and burn cultivation techniques on the forested ecosystems in particular and on environmental quality as a whole, in northeastern India.

STUDY SITES

Meghalaya is located south of Assam Valley and comprises the Garo, Khasi, and Jaintia Hills. The southern exposure receives an average annual rainfall of about 380 cm, but the annual precipitation at Cherrapunji exceeds 1 150 cm. At other places in Meghalaya average rainfall is as low as 200 to 230 cm. The flora is a subtropical humid type at lower elevations, and although Pinus kesiya is an important tree species at higher elevations, semideciduous broad-leaved forests seem to be the climax type as evidenced by the relict vegetation preserved in sacred forests.

The Naga Hills are a mountain range about 138 miles long and 25 miles broad with several over 1 750 m high. Vegetational types range from subtropical humid forests of lower elevations to temperate forests at higher levels. The average annual rainfall at Kohima is about 190 cm increasing eastward to a maximum of 280 cm.

The Mizo Hills located south of Manipur have a predominantly north-south axis and maximum elevations of 2 400 m are encountered in the Blue Mountain area in the south. The average annual precipitation ranges between 190 and 250 cm, but maximums of about 350 cm are reached in a few locations. The vegetation is humid subtropical to temperate depending upon elevation.

METHODS OF DATA COLLECTION

Vegetational analysis of Jhum fallows was done using a quadrat method. Thirty quadrats of 10 m² for trees and shrubs and 1 m² for herbaceous species were laid along a transect down the slope. The importance value index (IVI) is an integrated measure of relative frequency, relative density, and relative basal area and was calculated by the method outlined by Misra (1968). Diversity and dominance indices were determined using the formula given by Odum (1971).

Early colonizers were studied on a site at Burnihat which was slashed and burned in April 1977 and left fallow. Sampling for pigment analysis and studies on dry matter were performed periodically on 50 cm² plots where the species grows in pure stands. Chlorophyll pigments were estimated following the procedure of Holm (1954).

For studies pertaining to runoff water and sedimentation, the loss from a confined area of 1 x 10 m along the slope was collected in large drums of 200-liter capacity and periodically removed for analysis. Percolation studies were done using a simple lysimeter of the "Russian type" (Buckman and Brady 1960). The soil was cut out vertically to expose the profile. A small tunnel was excavated at a depth of 40 cm (the depth to which most roots penetrate) and a collector of 30 x 30 x 15 cm was placed inside the tunnel. The collector was firmly inserted into the undisturbed soil above. Water percolating through the soil was tapped into receptacles. This method was satisfactory for comparative purposes, although values may have been low.

NO₃^{-N} was estimated colorimetrically by the phenol disulphonic acid method and PO₄^{-P} was estimated by molybdenum blue method (Allen 1974).

JHUM AT BURNIHAT

Burnihat, in the Khasi Hills and about 90 km north of Shillong, is located at 26°N. and 91.50°E. The pre-Cambrian rocks are represented by gneiss, schists, and granites. The soil is red, sandy loam, and of laterite origin. The pH ranges from 5 to 7. Angle of the slopes generally ranges from 20° to 40°.

The rainy season in Burnihat extends from May to September during which 90 percent of the annual average rainfall of 220 cm occurs. Maximum temperature and humidity is also attained at this time. There is a mild winter during December-February and temperatures begin to rise during March and April; this is largely a dry period.

The Jhum pattern at Burnihat and at an elevation of 100 m is typical of the pattern in the northeastern region. The tribal population engaged in this form of agriculture at Burnihat are predominantly Garos whose Jhum is similar to the practice followed by the same tribe in the Garo Hills of this State.

Agro-Ecosystem

The forest is felled in December and January. Occasionally, a few large trees may be left intact, but usually branches are cut and some large boles removed from the site for fuel. The slash is allowed to dry during the rainless winter months and burned during March and April. Dried leaves and small twigs are burned in situ whereas large logs are piled and fired two or three times to ensure complete burning. After one or two showers in April and May, weeding is done and then mixed crops are sown by dibbling in the steep slopes with little other preparation of the fields. The average size of a Jhum plot varies between 1.5 and 2.5 ha for an average family of two adults and three or four children.

Jhum cultivation varies, depending upon how long fields are left fallow. The interval between cultivation may be as long as 20 or 30 years, or as short as 4 to 7 years. In a plot under a long Jhum cycle as many as 14 crops may be grown together and harvested at different times (table 1). Annual crops such as rice, maize, Sesamum indicum, and Setaria italica are mixed with perennials like tapioca and an occasional banana plant. Perennials are taller than annuals and are usually harvested later. A few tuberous crops like ginger and some vegetable crops like Colocasia anticorum and cucurbits are also grown. Ricinus communis is used for rearing silkworms. Weeds like Eupatorium odoratum and Imperata cylindrica may also come up along with tree and bamboo sprouts, but these are periodically slashed down. With the harvest of maize and Setaria italica in July, rice and Sesamum indicum get more space at the peak of their growing period. The successive harvests of the annuals during September-November not only create additional space for the remaining crops but also add organic material to the soil from decomposing plant debris.

In the second year, cereal crops are not planted because yields are greatly reduced after the first year of cultivation. Sesamum indicum, tapioca, banana, and a few cucurbits are grown during the second year. While Jhum is normally not used for more than 2 years without a fallow period, sometimes the same land may remain in use for another 3 to 5 years for banana cultivation.

Where the Jhum cycle is short, the yield of cereal crops is low and may be harvested the first year. Crops like Sesamum indicum, tapioca, and banana along with vegetable crops do better and are sometimes preferred. The site is abandoned after a single year of cultivation. Further, the agro-ecosystem here differs from the one under a long cycle due to predominance of noxious weeds like Eupatorium odoratum, Thysanalaena maxima (broomgrass), and Imperata cylindrica.

TABLE 1.--Crops grown on Jhum land at Burnihat

Species	Density (plants/m ²)	Sowing time	Harvesting time
<u>Setaria italica</u>	2.8	April	mid July
<u>Zea mays</u>	2.2	"	mid July
<u>Oryza sativa</u>	8.6	"	early September
<u>Lagenaria</u> spp.	0.7	"	"
<u>Cucumis sativa</u>	0.5	"	"
<u>Zingiber officinalis</u>	0.2	"	early October
<u>Sesamum indicum</u>	4.3	"	"
<u>Phaseolus mungo</u>	0.4	"	"
<u>Cucurbita</u> spp.	0.2	"	early November
<u>Manihot esculenta</u>	0.9	"	"
<u>Colocasia antioorum</u>	0.4	"	"
<u>Hibiscus sabdarifa</u>	0.5	"	early December
<u>Ricinus communis</u>	0.7	"	(perennial crop)

Mixed cropping is apparently an efficient way of utilizing rapidly dwindling resources in an effective manner by choosing mutually compatible species. This is an aspect which needs much closer study.

Secondary Succession Pattern

The pattern of secondary succession in fallows during the first few years varies considerably depending upon the Jhum cycle and agricultural practices as follows:

(i) Eupatorium dominated fallow--where underground rhizomes are weeded out during cultivation regardless of the cycle, particularly when cultivation is done for more than 1 year.

(ii) Imperata dominated fallow--under short cycles I. cylindrica rhizomes are abundant in the soil and this species coexists with Eupatorium odoratum.

(iii) Mikania dominated fallow--under short cycles and where M. micrantha is abundant due to its growth habit. This species may choke the fallow and other herbaceous weeds. The species forms a thick mat on the ground, striking roots wherever they come in contact with soil.

(iv) Saccharum dominated fallow--S. spontaneum grows less frequently at Burnihat as compared to the Garo or Mizo hills. Dominates under short cycle conditions where cropping is for less than 1 year and where weeding of rhizomes is not thorough.

(v) Borreria dominated fallow--B. hispida is a stoloniferous species having both prostrate and erect branches and rooting at nodes. It forms an interwoven mat and checks seedling establishment of other species. It usually grows where Imperata cylindrica and Eupatorium odoratum are weeded out.

(vi) Bamboo dominated fallow--Under short cycles and when cropping is done only during the first year, rhizomes of bamboo, Dendrocalamus hamiltonii, remain in the soil and sprout. Due to their rapid growth, bamboo sprouts soon suppress other herbaceous weeds.

Under a long cycle, the herbaceous early colonizers dominate up to about 5 years after which sprouts of Dendrocalamus hamiltonii take over. Regeneration is mainly from fire-resistant underground rhizomes which store reserve food. Regeneration of seedling populations also occurs, though sporadic. The dynamics of bamboo are interesting. The species progressively becomes dominant and reaches a peak in both density and frequency in a 20-year fallow. Regeneration from sprouts is steady up to about 20 years and then declines. Conversely, mortality progressively increased reaching a maximum in a 50-year fallow.

In a 20-year fallow, broad-leaved species which are shade intolerant such as Vitex peduncularis, Schima wallichii, Terminalia bellerica, Bauhinia alba, and Dillenia indica, are also frequent. In a 50-year fallow, besides a few shade-intolerant trees like Schima wallichii, others like Shorca robusta, Castanopsis indica, Gercinia cowa, and Eugenia communis also become established but none is able to achieve dominance in the community.

A study of secondary successional communities for diversity and dominance patterns indicates that there is little diversity in the early successional stages and it progressively increases up to a 50-year fallow. Dominance was maximum in a 5-year fallow where Imperata cylindrica and Eupatorium odoratum dominated. Though diversity and dominance are calculated using the number of individuals (Arhenius 1921; Gleason 1922, 1925), these functions are also being examined by taking biomass into consideration. Our results are in agreement with those of Mellinger and McNaughton (1975) who showed that species diversity increased and dominance decreased with progression of old-field succession in New York. These results also seem to be in general agreement with the basic hypothesis of Margalef (1963, 1965) that succession is accompanied by increased biological diversity and reduced dominance.

Water and Nutrient Cycles

Unless otherwise indicated, results in this section are based on analysis of a site under a 30-year cycle and left fallow for 5 to 10 years. Further, present studies are for the monsoon period, May-September, 1978.

In the months of March and April when burning of the slash is done prior to cultivation, dry ash may remain on the soil surface for a period of 2 to 3 weeks before the first monsoon shower arrives. During this period, because of frequent high wind velocities, ash is blown from the Jhum land to adjoining forest fallows. Studies of two freshly burned sites, one under a 30-year cycle and another under a 7-year cycle, indicate that as much as 47.0 percent in the former and 28.1 percent in the latter may be lost.

Water loss due to runoff and infiltration during the monsoon period is illustrated in figure 1. Since about 90 percent of the rain comes during this period, it is reasonable to assume that most losses occur during this period. In the agro-ecosystem, over 50 percent loss of water is accounted for by runoff and infiltration and this was drastically reduced in a 5- and 10-year fallow.

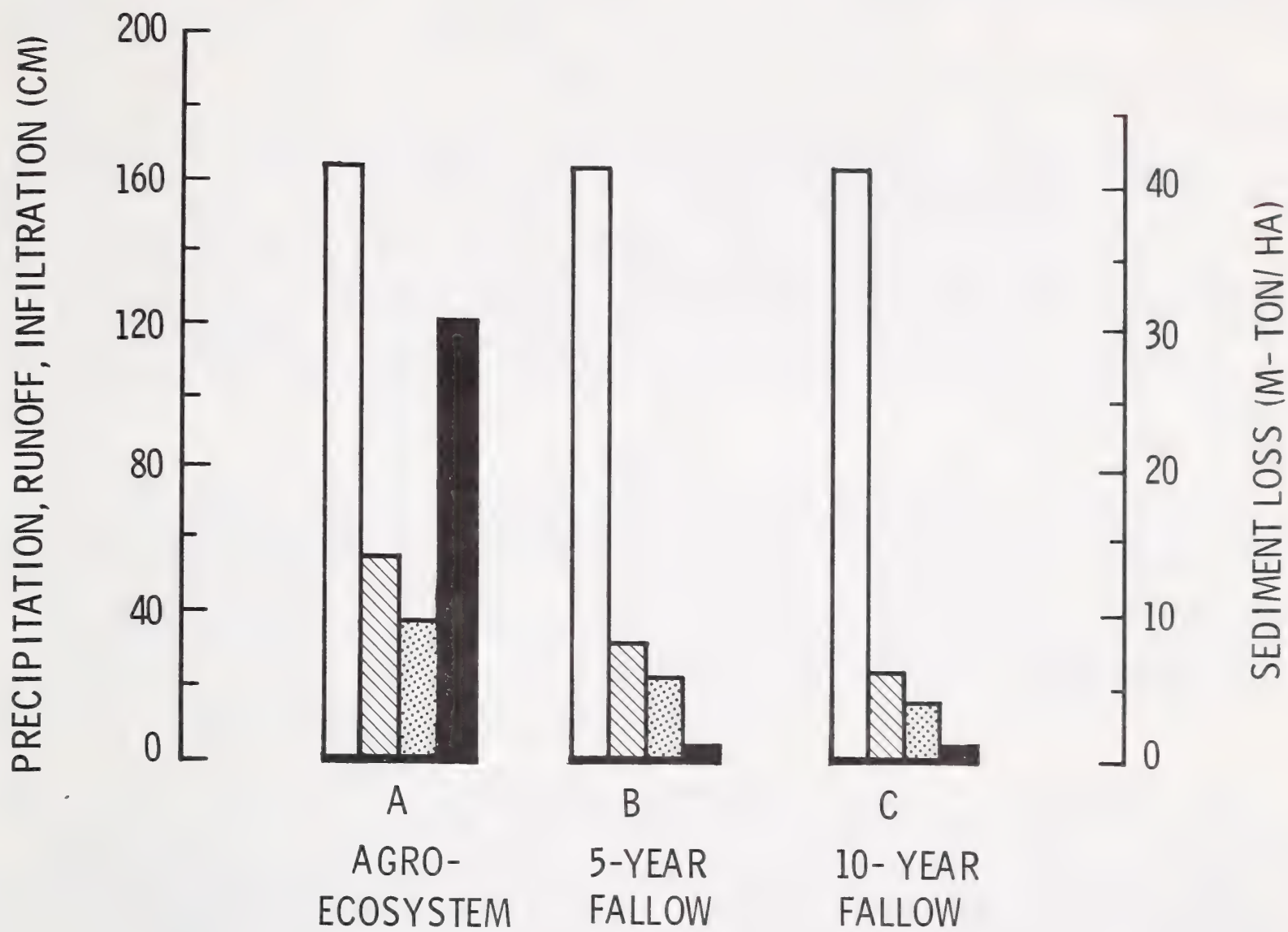


Figure 1.--Precipitation, runoff and sediment loss by land management practice at Burnihat.

Loss of particulate sediment in runoff dropped from 31 t/ha in the agro-ecosystem to 1.13 t and 0.76 t per ha, respectively, in a 5-year and 10-year fallow. In one of the 10-year fallows subjected to accidental burning from an adjoining area, sediment loss due to erosion was 19 t/ha.

Concentration of $\text{NO}_3^{-\text{N}}$ and $\text{PO}_4^{-\text{P}}$ in runoff and infiltrated water was higher in the agro-ecosystem and decreased with length of fallow. This relationship is also true for total loss of these two nutrients (table 2). Nitrate concentration and its total loss were much higher in the infiltrated water than in the runoff water. On the other hand, total loss of phosphate was much higher in runoff than in infiltrated water.

Loss of these two nutrients in the runoff water indicates that in the agro-ecosystem, the loss is maximum during May and June, declining sharply in subsequent months. This may be partly due to lack of established plant cover during the early part of the monsoon, since the crop had not yet attained proper size, and partly due to high nutrient release from ash as well as increased microbial activity soon after burning. Significantly, the pattern in a 5- and 10-year fallow indicates that the loss is steady throughout the monsoon for these two nutrients.

Loss of $\text{NO}_3^{-\text{N}}$ in infiltrated water also showed a similar trend. In the agro-ecosystem, a sharp decline in nitrate concentration was noted during the latter part of the monsoon. This trend was sustained in a 5-year fallow, though it was less pronounced. In a 10-year fallow, however, there was no significant fluctuation in nitrate concentration in different months. The $\text{PO}_4^{-\text{P}}$ concentration in different fallows did not fluctuate significantly during the monsoon.

JHUM AT SHILLONG

The Jhum pattern at higher elevations is significantly different from that of the typical type in the subtropical humid forests up to an altitude of 500 m, as exemplified by that at Burnihat. Shillong is located at an altitude of 1 496 m at 25.34°N . and 91.56°E .; here the slopes average 30° to 40° . Soils are gneissic derived from cretaceous formations. Of the two main soil types, laterite soils are reddish, and granitic derived soils range from light brown to dark brown. Soil texture varies from coarse- to medium-fine in the upper horizons to fine in lower horizons. Soil pH is between 4 and 6 but may be as low as 3.5 in pine forests.

TABLE 2.--Total loss of $\text{NO}_3^{-\text{N}}$ and $\text{PO}_4^{-\text{P}}$ in runoff and infiltration water under different fallows.

Fallow	Concentration (mg/l)				Total loss (kg/ha)			
	Nitrate		Phosphate		Nitrate		Phosphate	
	run-off	perco-lation	run-off	perco-lation	run-off	perco-lation	run-off	perco-lation
Agro-ecosystem	1.03	15.70	0.81	0.05	5.67	38.50	0.45	0.14
5-year	0.45	11.53	0.04	0.04	1.45	25.30	0.13	0.08
10-year	0.35	0.01	0.04	0.01	0.72	8.40	0.08	0.02

Shillong has a monsoonic climate with 90 percent of average annual rainfall of 215 cm occurring between April and September. Winter months are cold and extend from November to February. March is comparatively warm and dry with frequent strong winds, whereas the rainy season is relatively cool with high humidity.

Agro-Ecosystem

Jhum is practiced here mainly in areas where tree species are rather sparse. In thick forests, trees are felled in order to create large open areas where Jhum can be practiced; however, the destruction of the forest is not as thorough as at Burnihat. Part of the branches of trees, shrubs, and herbaceous undergrowth is cut and allowed to dry. Land is then worked into ridges and furrows which run along the slope, and slash is placed neatly on top of the ridges where it is allowed to dry during winter months. This prevents loss of ash due to blowoff from the strong winds at this time of the year. Cow dung is spread on fields as a supplement along with inorganic NPK fertilizer.

Upland rice, potatoes, or maize are grown on ridges, usually as pure crops, for 1 or 2 years. Occasionally potatoes and maize may be grown as mixed crops. Subsequently, vegetable crops like cauliflower and cabbages will be grown for another 2 or 3 years. The fields are usually returned to fallow after 5 to 6 years of cropping.

The preparation of the land into ridges and furrows and more discrete destruction of plant cover through controlled burning are some of the advanced features of the agro-ecosystem. These activities and the application of cow dung or inorganic NPK as a fertilizer supplement are evidence of a modified form of agriculture more closely resembling a sedentary agro-ecosystem.

Secondary Succession

Since tree species are not completely destroyed, secondary succession is initiated in openings between older trees. Early colonizers are chiefly herbs and some shrubs. Species like Eupatorium adenophorum, Imperata cylindrica, Osbeckia crenata, Gleichenia linearis, and Anaphalis contorta are important early colonizers. In a 5-year fallow, in addition to Eupatorium adenophorum and Imperata cylindrica, Eupatorium riparium, Saccharum spp., Lantana camera, Rubus spp., etc., are prominent with such tree seedlings as Pinus kesiya and Quercus spp. In a 10-year fallow, a number of tree species including Pinus kesiya, Schima wallichii, Rhus spp., Lindera spp., and Callicarpa macrophylla attain heights of 8 to 10 ft and the undergrowth may be comprised of many of the herbs and shrubs found in younger fallows.

Water and Nutrient Cycles

In the agro-ecosystem where potatoes were cultivated as the crop, about 35 percent of the annual precipitation is lost as runoff. This loss declines drastically with the length of the fallow period. Infiltration, on the other hand, increased in a 5-year fallow and decreased slightly in a 10-year fallow. The sediment yield in the agro-ecosystem is 39.3 t/ha but dropped markedly to 3.45 t/ha in a 5-year fallow and to 1.92 t/ha in a 10-year fallow (fig. 2). These values are comparable to the soil losses in an untterraced rice agro-ecosystem in the humid mountains of Java where it was found to be 49.4 t/ha/yr (Gonggrijp 1941).

Distribution of sediment losses is closely related to rainfall during the monsoon; the steep rise in sediment loss in September is related to the disturbance of soil during harvest activities. In the two fallows, sediment loss is low and is chiefly confined to the early part of the monsoon season.

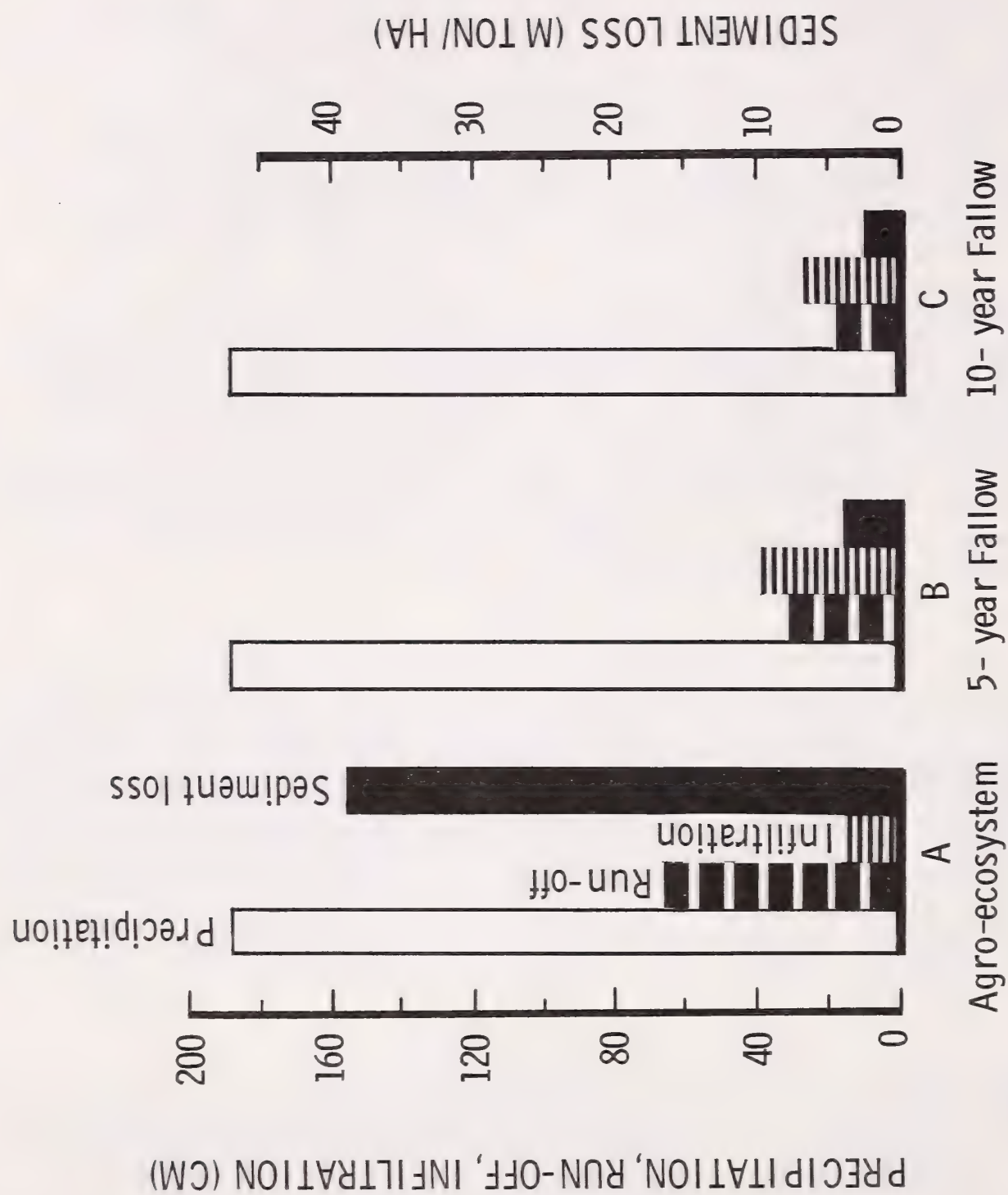


Figure 2.--Precipitation, run-off, infiltration, and sediment loss by land management practice at Shillong.

The loss of runoff is similar to the pattern of sediment loss in the agro-ecosystem. Infiltration loss of water was maximum during June, probably related to rainfall and also the development of plant cover on the soil surface.

The concentration of $\text{NO}_3^{-\text{N}}$ in sediment was much higher compared to runoff and percolated water. The concentration of this nutrient was higher in infiltration water compared to runoff in the agro-ecosystem and 5-year fallow. However, total loss per hectare was more through runoff than through infiltration loss. Infiltration of this nutrient was maximum in a 5-year fallow, though sediment and runoff was maximum in the agro-ecosystem (table 3).

The $\text{NO}_3^{-\text{N}}$ concentration in eroded soil declined markedly during the latter part of the monsoon in all fallows. Differences in concentration in the three fallows were more pronounced in the early part of the monsoon. The same pattern was discernible in total loss of this nutrient. However, the slight rise in $\text{NO}_3^{-\text{N}}$ in eroded soil during September is probably due to very high sediment loss during potato harvest. In any case, the loss was much higher in the agro-ecosystem compared to other fallows.

Nitrate loss in runoff showed a steep fall in concentration during the latter part of the monsoon for the agro-ecosystem only. There were two peaks in total loss per hectare, one in May when rainfall was high and crop cover was not yet effective and another during September when the crop was harvested and plant cover was absent.

The concentration of $\text{NO}_3^{-\text{N}}$ in the percolated water in all three fallows declined during the latter part of the monsoon; and this decline was most evident in the agro-ecosystem. However, total nitrate concentration in infiltration water peaked during May and June though not as sharply in a 10-year fallow.

TABLE 3.--Total loss of $\text{NO}_3^{-\text{N}}$ due to sediment, run off, and percolation in different fallows at Shillong.

Fallow	$\text{NO}_3^{-\text{N}}$ concentration (mg/l)			Total loss (kg/ha)		
	Sediment	Run-off	Percolation	Sediment	Run-off	Percolation
Agro-ecosystem	1.37	0.35	0.54	0.067	2.49	0.72
5-year	1.00	0.25	0.38	0.007	0.73	1.17
10-year	0.70	0.19	0.18	0.003	0.34	0.36

OTHER JHUM PATTERNS

Jhum practiced by the Garos in the Garo Hills of Meghalaya is similar to that at Burnihat previously discussed. Where population density is higher, the cycle may be only about 4 or 5 years whereas in the less densely populated interior part of Garo Hills the cycle may be longer.

In the Mizo Hills, land is subjected to intensive Jhum and the cycle is often very short. The entire forest is in a highly degraded form, often maintained in early successional stages, and the landscape is predominantly bamboo forest with such species as Melocanna bambusoides, Bambusa tulda, and Dendrocalamus longispathus.

In Nagaland, Jhum is similar to that at Burnihat. The cycle is shorter, often about 3 or 4 years, largely because of higher man/land ratio. As a consequence, Eupatorium odoratum readily establishes itself and vast stretches of land are almost a monoculture of this species. Imperata cylindrica and Saccarum spontaneum are also common amongst early successional species.

ECOLOGY OF EARLY COLONIZERS

Large tracts of land in the hill areas of the northeast are dominated by exotic species, Eupatorium spp., Mikania mucronata, Imperata cylindrica, Thysanolsena maxima, and Grewia elastica. This presents a major problem from an agronomic viewpoint.

The success a species may possess depends upon the strategy it may adopt in its exploitation of available environmental resources. In a newly burned area which has been under Jhum for sometime, the success of an early colonizer depends upon its ability to colonize the steep slopes at a fairly rapid rate and thereby conserve the nutrients which are otherwise difficult to capture and retain at a given site. A species may be successful either through heavy seed production combined with efficient seed dispersal or through effective vegetative propagation or both.

Of the four species which have been studied, Eupatorium odoratum and Thysalonaema maxima produced seeds profusely during the first year after being left fallow. Average seed production of E. odoratum at low elevations and E. adenophorum at high levels are on the order of 48,000 and 380,000 seeds per plant under noncompetitive conditions. Imperata cylindrica and G. elastica did not flower at all during the first year, though flowering was observed in ecological situations not subjected to fire. Abrahamson (1975) noted that on sites where clonal expression of populations is predominant, a large proportion of resource is utilized in vegetative propagation. This strategy is probably at work in the case of these two species, too, suggested by preliminary observations of their energy allocation pattern.

In the case of vegetatively propagated species, survival and regeneration of plant species depends upon the distribution of reproductive organs under the soil. The deeper and more extensive the underground organs, the greater will be the survival rate, particularly after a fire. The survival of I. cylindrica, T. maxima, and G. elastica, which primarily come up by sprouts during the first year, is due to strong rhizomatous systems in the former two grasses and a deep-seated root system from which sprouts emerge in the third species.

The success and spread of two introduced species of E. odoratum at low elevations and E. adenophorum at high altitudes is due partly to the extreme plasticity of the former and the presence of altitudinal ecotypes in the latter. Thus, populations of E. odoratum from Burnihat (100 m) and Barapani (700 m) did not show significant differences when grown at Burnihat in a neutral substratum. However, E. adenophorum populations taken from Barapani (700 m), Shillong (1 500 m), and Upper Shillong (1 750 m) and grown in a neutral substratum under Shillong conditions showed marked differences in both vegetative and reproductive growth. More work is in progress to elucidate the significance of plasticity vs. genotypic response to the environment in the adaptational ecology of these species.

An important effect of fire on soil characteristics is related to increase in the rate of nitrification (Nye and Greenland 1960). A stimulatory effect of nitrate on the germination of seeds of E. odoratum is likely to be advantageous to the survival of this species. Our studies on germination indicate such an adaptation (Saxena and Ramakrishnan, unpublished).

Another important adaptive feature of early colonizers is their ability to make efficient growth so that they may overcome the limitation imposed by small-sized seeds and limited food reserves (Bazaz 1975). Taking grams biomass per milligrams chlorophyll at the height of the growing as an index of production efficiency (Bray 1968), we found that E. odoratum is four- to eightfold more efficient than I. cylindrica, strongly suggesting that this strategy offsets considerably the initial disadvantage of minute seed size.

SOCIO-ECONOMIC CONSIDERATIONS SUSTAINING JHUM

Slash and burn agriculture is a way of life with the hill tribes of northeastern India. The social life of tribes of this region is regulated by the Jhum calendar. Celebrations of various festivals, social and religious, coincide with different operations of Jhum cultivation. In the northeastern region, there are about 150 tribes and each has its own ceremonies, rites, and festivals associated with shifting agriculture.

Lue Kapha is a festival celebrated by many Mizo tribes. Literally, it means the search for a new field. During this time they select an area and invoke the gods. After returning home, if the chief of the village has a good dream then the site selection is good, otherwise a new slope is selected.

Agalmaka is a festival among Garos of Meghalaya that marks the cutting and burning of the forest. Feasting accompanied by dance and songs is involved. This festival is also meant for pleasing the forest gods so that no one suffers any misfortune during this period. Khua-Nu is the name of mother nature and is worshipped by the Mizos at this time. Kang-Ral-Ni is a traditional mourning day for the Mizos, for the creatures who die in a Jhum fire.

The sowing period is usually preceded by two important ceremonies like Gitchipong and Michiltata amongst the Garos. The former is a family sacrificial function whereas the latter is a collective ceremony in which the whole village participates. On this occasion, Rokime, the mother of rice, is propitiated.

Before sowing, the Khasis of Meghalaya observe two ceremonies: Puh-dain and the Nongkrem ceremony. These ceremonies are directed toward a successful cropping season. The Mizos sacrifice a black hen on Jhum land at the time of sowing; a few seeds are smeared with its blood and are sown near the place of sacrifice. The Sema-Nagas celebrate Aokhuni after sowing. If rain is wanted they propitiate the rain god. The crab is associated with rain, both among the Garos and the Sema-Nagas, and the ceremonies are often centered around this animal. Wanchos of Arunachal Pradesh celebrate sowing time by sacrificing fowl, sprinkling the blood in the fields, followed by feasting and dancing.

Kashong-Kahao is a festival celebrated by Tangkul Nagas to ward off dangers to standing crops from insects and pests. Ma-won-Zai is held when ears appear on rice plants. Animals are killed and prayers said for protection of the crop. Miamua is an important festival among the Garos during flowering time of rice crops. Sacrifices of pigs and fowls are made followed by feasting and drinking rice beer.

The Garos of Meghalaya have the Wangala, which is one of the big festivals, and is known as the 100-drum dance. Fowl, pigs, and ducks are offered as sacrifices to the sun god, Laljong, who is known to be the source of all energy. This is accompanied by feasting, drinking, and dancing. Pawl-Kut is a festival of Mizos to mark the end of the harvest and to welcome the new year.

After harvest, very often, gods are propitiated to protect the granary. Many Naga tribes have sacrificial offering to the goddess of wealth by cutting a fowl and throwing its flesh in the direction of the supposed abode of the goddess.

These ceremonies discussed here are only a select few of festivals celebrated by different tribes of northeast India. There are many more. In short, all social and cultural patterns of these tribes are closely woven into and are centered around traditional agricultural operations. Among many tribes, the homecoming of newly wedded brides and other social ceremonies are conducted at the festivals.

Table 4 shows the area under Jhum and is based upon data compiled by the North-eastern Council, Shillong. These figures are based on the assumption that only a certain acreage is under cultivation in any given year and that the cycle is of a specific duration. However, they ignore the reality that the area under shifting agriculture is not always the same, but is changing because of gradual impoverishment of the fallows, changes in the amount of land available for Jhumming, and other related factors. Therefore, the total area carrying degraded vegetation is many times more than that which has been assumed.

The Agro-Economic Research Centre, Jorhat, Assam, conducted surveys on Jhum yield of rice and concluded that 800-900 kg/ha in Garo Hills, Mizoram, and Arunachal Pradesh is comparable to the average yield of 1 145 kg/ha for the country as a whole for 1971-72. This, of course, does not include the yield from a number of other crops from the same land (quoted by Misra 1976). In a recent study of the socio-economy of shifting agriculture and its control, Aurora and others (1976) concluded that the yield of rice under Jhum and dryland cultivation on terraces is not significantly different, under comparable situations. However, according to an unpublished report of the Indian Council of Agricultural Research (Borthakur and others 1978), the yield under Jhum is very low compared to terrace cultivation. Unfortunately, they do not specify inputs under terrace cultivation, or indicate the Jhum pattern, or the mixtures of crops under Jhum compared to monoculture of rice in terraces. Thus, the report of 190 kg/ha under Jhum cultivation and 1 860 kg/ha for terraced agriculture is not comparable. The cultivation on terraces was done with input of fertilizers.

Table 4.--Area under Jhum based upon data compiled at the North-Eastern Council in Shillong

		Area under Jhum (1 000 ha)			
State	Geographical	Annual percent		Total percent of	
		geogr.		geogr.	
----- area -----					
Arunachal	8149	92	1.13	248	3.04
Assam Hills	1535	70	4.56	498	32.44
Manipur	2236	60	2.68	100	4.47
Meghalaya	2253	76	3.37	416	18.46
Mizoram	2108	62	2.94	604	28.65
Nagaland	1649	74	4.49	608	36.87
Tripura	1067	23	2.16	221	20.71

In conclusion, it may be pointed out that the results obtained by different workers quoted above are confusing, particularly in view of the absence of details regarding agricultural practices and crop yields, resulting in questionable validity of the conclusions. However, it is clear that one of the main economic considerations which sustains Jhum is the cheaper inputs for a given yield.

GENERAL CONSIDERATIONS AND CONCLUSIONS

Preliminary results of our study indicate that Jhum cultivation has caused large-scale degradation of the environment. Most of the forests in the region are degraded and are fallow, 3 to 20 years old, extending over vast areas of the hills of northeastern India. In fact, natural forest stands 50 years or older are rare in Meghalaya. However, the local population, for cultural reasons, has maintained small patches of "scared forests" which indicate the type of climax forests in the region.

There are indications, on the basis of crop yield (Pakem and others 1976), that a long cycle of about 15 to 20 years ensures stability of the system, does not cause environmental deterioration, and achieves a balance with conditions of soil, vegetation, and climatic characteristics of the area. Zinke and others (1978) working on Lua forest fallow system of shifting cultivation in Thailand suggest a 10-year cycle for such a stability of the ecosystem. According to them, as also observed during the present study, short cycles have resulted in inadequate restoration of soil fertility.

The takeover of Jhum fallows by weedy colonizers like Eupatorium odoratum and Imperata cylindrica under short cycles has resulted in rapid deterioration in the environment. Succession has been arrested indefinitely at this pioneer stage. This has also been noted under Lua forest in Thailand where Eupatorium odoratum is a predominant weed (Zinke and others 1978). In the superhumid regions of southeast Asia and central Africa, 1 to 2 years of cropping is normally followed by 10 to 20 years of fallow. This extended fallow is needed to control Imperata cylindrica (Nye and Greenland 1960). However, according to the same workers, short cycles with a longer cropping period are feasible in less humid forests and the savannas of Africa. This apparently permits stable conditions in both these situations.

When the cycle is short, hazards of erosion are considerable even though the land is colonized by weedy species and the likelihood of accidental spread of fire hazard is increased because of the high susceptibility of Imperata cylindrica. In fact, in one study of a 10-year-old fallow subjected to accidental ground fire, sediment loss was found to be as high as 20 t/ha during the monsoon.

A comparison between the more traditional form of Jhum at Burnihat and the variant at Shillong indicates that damage in the latter case is in no way less severe. In fact, sediment loss due to erosion in the agro-ecosystem under conditions at Shillong is more severe than at Burnihat. The lesser damage at Burnihat might be attributed to (a) a more rapid regeneration of vegetation under the hot, humid climate; (b) least disturbance in the soil structure as the land is not plowed, and (c) poor weeding practices.

Damage to the ecosystem could best be exemplified by an extreme case of Jhumming at Cherrapunji, which is well known for being one of the highest rainfall regions in the world. The annual average exceeds 1 150 cm and an above-average year may bring as much as 2 250 cm, recorded during 1974. Most of this rainfall comes between May and September. In spite of high rainfall, one is struck by the general barrenness of the landscape. Most of the area is denuded, characterised by bare rocks jutting out and a few dwarf grass species like Chrysopogon, Cymbopogon, Eragrostis, Panicum, and Paspalum surviving in a thin layer of soil. However, Cherrapunji has a small patch of relict forest at Mawsmi and other patches in more protected valleys with rich species diversity. These areas contrast dramatically with the largely degraded landscape. The forest at Mawsmi has Quercus spp., Castanopsis spp., Schima wallichii, with a large number of shrubs like Photinia, Eriobotrya, Pyrus, and Prunus. An obvious conclusion is that these forests were destroyed over a period of time, possibly through Jhum cultivation. The evidence for this conclusion is twofold: (1) the local people practice Jhum and (2) Jhum lands are extensive in the forested area around Cherrapunji.

In any case, due to damage to the ecosystem, there is scarcely any vegetational cover to hold the soil and there is no soil to support a forest.

As mentioned earlier, exotic weed species have created a serious problem in weed control due to their rapid spread under a short Jhum cycle. This has resulted in the rapid depletion of the germ plasm, because of drastic changes in microclimate and other elements of the habitat. Many orchid species of Dendrobium, Cymbidium, and Vanada are on the endangered list of plant species.

The forested areas in Meghalaya ensured the survival of a rich mammalian fauna. In fact, more than 50 percent of the total number of mammalian genera known from the Indian subcontinent are represented in this region. Because of destruction of forest, chiefly for Jhum, the habitats of these animals have been damaged. A large number of species once distributed over large areas in this region are now on the list of protected species, e.g., eluded leopard (Neofelis nebulosa), golden cat (Felis temmincki), leopard cat (Felis bengalensis), tiger (Panthera tigris), wild buffalo (Bubalus babalis), etc.

As discussed earlier, Jhum is a way of life with the tribal population of the hill tracts of northeastern India. The pattern of cultivation in this study as in other parts of the world (Nye and Greenland 1960) is governed not only by soil fertility but also by the whole social, historical, and environmental setting of the people and their aim to get maximum return for minimum effort. This age-old practice was previously in harmony with nature, but in recent times, because of population pressures and limited areas available for Jhumming through changes in the land tenure and other government policies, the practice cannot be sustained, for obvious reasons.

Population pressure determines the fallow period. This is further complicated by the settlement pattern of people. In more primitive societies such as the aboriginal Sakai in Malaya (Dobby 1942), people are less attached to their dwelling sites and are mobile. In more advanced societies, as in the present situation, they are more attached to their dwellings. This is leading to more intensive farming near settlements which leads to faster deterioration of the environment. Slopes are steeper in the northeastern region compared to many other parts of the world where shifting agriculture is done, for example, many parts of Africa (Webster and Wilson 1966). Rainfall is high through parts of Africa particularly in the moist evergreen zone; southeast Asia may have equally high rain fall. These regional characteristics, along with population pressure and weed problems discussed earlier, affect the method of shifting cultivation. Further, short cycles of Jhum affect soil fertility and the ability of the soil system to recover. Watters (1971) even suspects that the tropical American soils are more fertile compared with major African and Asian soil types, which needs to be looked into more carefully.

However, replacement of Jhum by intensive agricultural practices is probably not a realistic solution to this problem either. As a solution to the problem, the Indian Council of Agricultural Research station at Shillong has suggested partial terracing with horticulture and forestry development on the upper two-thirds of the slopes (Borthakur and others 1978). They claim that runoff was reduced from 144 mm to 8.1 mm and sediment loss was reduced from 40.9 t/ha to 5.8 t/ha through terracing. However, it is suspected that concentration and total loss of nutrients in runoff and percolated water is likely to be very heavy, particularly in view of heavy fertilizer inputs.

Agriculture is a necessary land management practice in the hilly regions and it is no doubt not practical to completely eliminate Jhum, but restrictions and modifications of this age-old practice to minimize damage to the environment from a long-term point of view are imperative. Modern agriculture, as we know it today with heavy fertilizer inputs, is likely to create more problems than it would solve. It may be desirable to keep cereal cultivation to a minimum and encourage horticulture and other

perennial crops. These would cause less damage to the environment. From an ecological point of view, one may go so far as suggesting importing grains into this region. The local economy may be developed in other directions, e.g., intensively growing horticulture and plantation crops.

In relation to the rest of the Indian subcontinent, the geographical positioning of the Himalayas and other extension ranges, like the hills of the northeast, is unique. We cannot afford to significantly alter, much less damage, the ecosystem because all major river systems originate from these mountains and drain into the northern plains of the country. Therefore, any damage to the ecosystem of these mountains would have repercussions over a large area of the plains. These repercussions might be: floods, deposition of silt, or major changes in the climate of the subcontinent. Record floods in the Ganga basin in 1978 were related to extensive deforestation in the Himalayas.

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FIRE POLICY AND ECOSYSTEM MANAGEMENT

INTEGRATING SUMMARY

This conference was organized to discuss the role of fire over a broad spectrum of fire cycles and intensities. It was planned to determine, in an objective manner, general principles of the functional role of fire in the development of ecosystems in time and space, adaptations of plants to fire, and the role fire has played in affecting ecosystem processes. Fully recognizing that land management is the link between the ecosystem and society, this last section was designed to see how knowledge of fire's role in the ecosystem is being put to use.

The conference is timely. Public land agencies are changing traditional policies of suppressing and using fire. A relatively new term, fire management, has been used to describe some of these changing approaches to fire. Barney (1975) defined fire management as "the integrating of fire-related biological, ecological, physical, and technological information into land management to meet desired objectives". . . in short, to utilize scientific fire information in land management. Fire management activities must be governed by land management objectives, be sound from ecological and economic viewpoints, and be evaluated for both beneficial and harmful effects.

These changes may be earth shaking to large, long established fire organizations. It has not been without controversy. However, it behooves scientists and land managers alike to approach the problem with an objective, scientific rationale. We cannot do otherwise. Hence, the significance of this conference. F. H. Bormann pleaded with the group at the onset to approach the subject with objectivity. And this has not always been the case with fire activities. We have had our share of extremists--both revolutionary advocates and stubborn reactionaries. What fire management needs is objective analyses and pertinent facts. And to counter the extremists, we need a large dose of common sense.

The final section has examined how fire is being handled by land management. Each speaker has contributed to our goal of how our knowledge of fire cycles and intensities are being managed by land management and the public.

David Parsons, in his paper "The Role of Fire Management in Maintaining Natural Ecosystems," began by discussing fire management as a tool in maintaining natural ecosystems. There is a significant distinction between using fire for maintaining natural ecosystems and using fire to meet specific land management objectives (particularly to favor particular plant or animal species). An example of the former is to permit fire to play a more natural role in a large ecosystem such as in National Parks or Wilderness Areas. An example of the latter is to improve winter range for maintenance of an elk herd. Whereas Parsons concentrates on the former, William Niering's paper discusses the latter. Another distinction is that the use of fire may be either through prescribed fires with natural ignition or prescribed fires with deliberate ignition, i.e., traditional prescribed burning.

To understand appropriate uses of fire, one must have insight into fire's role in natural ecosystems. Interested parties should consider historical evidence, biological evidence, and impacts of fire suppression. Fire has had considerable influence on natural ecosystems and we must understand something of the nature of this before we develop a fire management program to maintain fire's role in naturally functioning ecosystems. When measured today, the historic role of fire also includes the effects of past, aggressive fire suppression policies.

Once the rationale for using fire in natural ecosystems has been established, one is left with the realities of implementation. Dr. Parsons discussed alternatives to consider in implementing fire management programs and provided us with information on how to develop a fire management program. A most critical part of this procedure is the development of management prescriptions. We need to know what kind of fire we want and how to keep it that way. The prescription should contain two major elements: (1) an estimate of potential fire behavior and (2) a prediction of fire effects. Thus, the data required to write prescriptions should be those necessary to estimate a particular kind of fire and those needed to predict the effects of that fire. It is more complex than some standardized measure of fire intensity alone. Many factors influence fire effects--preburn conditions, an array of the fire characteristics, and postfire environment. The bottom line is whether the fire can achieve desired management objectives. Further, achievement of management objectives should be within tolerable limits of off-site effects.

Large, complex computer models are sometimes used in prescription writing and planning, e.g., those developed by Rothermel (1972) and Kessell (1979). Although useful for gaining insights to fire behavior, current fire modeling procedures are inadequate for much of the prescription writing or for planning purposes.

Current fire modeling procedures accurately predict rate of spread in uniform fuels such as grass and some shrub types (Rothermel 1972). Therefore, in some areas such as in the Mediterranean-climate regions of the world we have excellent fire prediction models. In many forested regions, the fire of great consequence is the large, high-intensity conflagration. It is exactly this kind of fire for which our fire organizations have won political support and for which we can least predict fire occurrence and behavior. We must learn more about the variability of nonuniform and large-sized fuels and the occurrence and behavior (including spotting and crowning) of fires in these areas. Furthermore, from a planning context we need information on the variability of fuels on the ground, probable patterns of fire weather, and probabilities of ignition and behavior. This will place more emphasis on statistical inference and stochastic methods rather than on deterministic approaches to fire modeling. Linking fire occurrence and behavior to fire effects is paramount and will call for a closer working relationship between traditional fire researchers and those studying forest and range ecosystems in a systems framework.

William Niering in "The Role of Fire Management in Altering Ecosystems" reported on the use of fire to meet specific land management objectives. He discussed several ways of using fire in wildlife, forest, and range management, and in maintaining biotic diversity. An important relationship involved in all of these uses is to determine the complex response of vegetation succession to fire regimes. It is important to understand natural succession with and without fire and to understand the past role of fire in altering the ecosystem to meet specific land management objectives. Dr. Niering points out the need to reevaluate our traditional Clementsian views of succession and climax as these terms apply to our interpretation of fire-influenced ecosystems. The change in vegetation triggered by fire is complex and to thoroughly understand its nature, we must understand the prefire situation and trends, the function of fire frequency and intensity, and the impacts of the postburn environment.

Dr. Niering defines prescribed burning as the skillful application of fire to the fuel complex that will confine the fire to a designated area and produce an intensity of burn to accomplish certain planned land management objectives. Fire can be used to remove unpalatable growth, to control unwanted plants or disease, to lessen fuel hazard, or to create or maintain environmental conditions to favor certain populations of plants or animals.

One of the most useful applications of fire is to provide specific habitat conditions required by wildlife. In fact, it is probably one of the most important management tools to improve wildlife habitat currently available. Dr. Niering's paper contains example after example of using fire for this purpose. Beginning with Stoddard's classical studies in bobwhite quail, Dr. Niering enumerates the role of fire in the management of such species as ruffed grouse, prairie chickens, sage grouse, moose, elk, deer, fur bearers, and waterfowl. Uses of fire as a tool in forest management include site preparation, altering species composition, and fire hazard reduction. Traditionally, fire has probably been used more for hazard reduction and site preparation than any other use in forest management. Thousands of acres are burned annually following logging.

A more subtle use of fire is its role in providing biological diversity. Using fire to provide biological diversity is particularly important in maintaining natural ecosystems for scientific study and in providing gene pools for maximum genetic potential in the future. We must maintain a long-range, holistic view in evaluating this use of fire as well as for specific land management objectives. If fire is to be managed, it must be directed and controlled. And it can be managed to meet a multitude of uses, both practical and altruistic.

A question that I feel needs particular attention is the role of fire in the maintenance of the vast array of ecosystems in Research Natural Areas (RNA). Federal land management agencies have nearly 400 Research Natural Areas covering 4.4 million acres. Two primary purposes for developing a system of Research Natural Areas are:

1. To preserve a representative array of all significant natural ecosystems and their inherent processes as baseline areas. This policy provides a potential range of diversity, including common, rare, and endangered species or disjunct populations.

2. To obtain, through scientific education and research, information about the components of natural systems their inherent processes, and comparisons with representative manipulated systems.

The underlying emphasis in RNA management is on preserving and protecting features of each area by controlling any disruptive use, encroachment, and development. Activities such as logging, grazing, burning, or restocking are prohibited unless the activity replaces natural processes and contributes to the protection and preservation of the designated feature. Such a practice is invoked only after thorough research and testing indicate that it adequately or favorably benefits the feature. In such an instance, a portion of the tract is left untreated as a control to justify the practice.

RNA ecosystems vary from seral to climax stages of succession, and most certainly, no one overall fire management practice should prevail. There should be an equally vast array of fire treatments to meet the varied requirements of research natural areas. Where might natural, prescribed fires be used? What levels of protection are required? I believe that we must approach this subject with care, keeping in mind the role fire has historically played in each area and the purpose or particular feature of the area set aside.

An equally intriguing question is the role of fire in preserving rare and endangered species, plant and animal. What is fire's role and what are our objectives? What is needed is specific information on habitat requirements and fire effects.

Another area with much potential, some already realized, for using fire is in rangeland management. Millions of acres of rangeland are burned in Texas each year. In California fire has been used to convert chaparral to pasture. However, many of our public agencies are just beginning to use fire for improvement of range ecosystems

and the potential for using fire for this purpose is great. In recent years the Fire in Multiple Use Research, Development, and Applications Program located at the Intermountain Forest and Range Experiment Station's Northern Forest Fire Laboratory in Missoula, Mont., has provided the U.S. Department of the Interior, Bureau of Land Management (BLM) with prescribed burning guidelines and training in burning techniques. Several BLM districts in Nevada, Idaho, and Utah and elsewhere have begun pilot tests in operational burning programs to improve rangelands for both livestock and wildlife.

Scientific knowledge has played a major role in the use of fire to alter ecosystems. Knowledge about fire frequency and intensity is a key factor in providing answers on fire effects for these purposes.

The efficacy of fire suppression activities is an important consideration in evaluating and planning fire management activities. What effect has fire suppression had in altering forest and range ecosystems? J. Harry G. Smith in "Fire Cycles and Management Alternatives" illustrated possible impacts of fire suppression on forest age class structure in British Columbia. Although his study deals more with fire frequencies than intensity, it does address relative changes of species distribution by age class with time. The primary interests of British Columbia forest managers have been in reducing fire occurrence, decreasing fire control response, and diminishing fuel hazard. They have a pragmatic interest in determining levels of protection over a region with vastly different fire regimes. Early records showed that volumes lost by fire were far greater than volumes removed by logging, e.g., in 1881 fire losses were 32 times the volume removed by logging. Recent fire losses have been considerably less than volumes removed by logging.

Dr. Smith used stand age to determine fire cycles and presented data on percentage of area burned and fire cycles by species groups. Two primary results are evident. Since the implementation of fire suppression the number of acres burned has been reduced and fire cycles have increased by a factor of 100 to 1,000 times. Species composition has been drastically altered. Generally, seral species have decreased at the expense of climax species. Dr. Smith demonstrated the utility of fire cycles in establishing levels of protection and showed the effectiveness of past fire control efforts in British Columbia forests.

Impacts of fires beyond the area burned have a significance beyond traditional damage appraisals. Art Tiedemann summarized the problem of evaluating off-site effects of fire in his paper on "Regional Impacts of Fire." In evaluating effects of fire upon an ecosystem, it is easy to ignore an evaluation of impacts outside the boundaries of the management unit. Yet, it is these impacts which might very well jeopardize ongoing fire management programs. Activities resulting from new fire policies in public agencies and attempts to use fire for management objectives on private lands may be hampered by potential negative off-site effects. Dr. Tiedemann identified and characterized some significant off-site effects of fire. He concentrated on smoke, esthetic impacts, economic consequences, and watershed effects.

Obvious impacts of smoke emissions include visibility impairment and health problems. More subtle impacts include light attenuation affecting fruit production and other effects on adjacent plant communities. Although we have begun to develop technology to burn effectively and still conform to environmental laws (Southern Forestry Smoke Management Guidebook by Mobley and others 1976), there is still a need for knowledge to burn effectively to achieve land management objectives while minimizing impacts of the fire on air quality.

Esthetic impacts of the result of fire are more difficult to measure because human attitudes are involved. There is still a strong feeling that fire may have considerable negative impacts on esthetic quality. A central question remains: are people willing to accept short-term negative aspects (smoke pollution) to attain long-term benefits

(wildlife habitat improvement). Economic consequences of a fire management program are extremely complex. Dr. Tiedemann used the 1970 Entiat Fire in Washington to illustrate the far-reaching economic impact of an altered timber base and postfire impact on sight seeing, hunting and fishing, fruit production in the valley, and water production. We have only begun to use such analyses to evaluate fire management. Today's management complexities, however, require us to do so. This complexity is overwhelming, but we must not ignore it. It could mean the difference between success and failure of fire management programs.

An excellent example of the complexities of off-site impacts and how social and economic considerations influence application of scientific information is found in Dr. R. P. Ramakrishnan's case history of the practice of Jhum in India. Dr. Ramakrishnan and his colleagues at Northeastern Hills University in Shillong, India, presented the paper, "Slash and Burn Agriculture in Northeastern India." Their studies describe environmental impacts of a land management practice, brought about by strong social and economic factors. This practice called Jhum is long established and consists of slashing forested sites, burning them, and then planting a mixed crop. They are studying such environmental processes as secondary succession and water and nutrient cycling.

Jhum is a way of life for these hill country tribes. Their social life is regulated by the Jhum calendar. Their Jhum practices are blessed by the diety, Misipa. Although not as efficient for production of particular crops, the practice permits a diversified approach to tribal needs and inputs into the system are relatively inexpensive for a particular yield. The practice is entrenched and politics are not conducive to any change regarding the practice. However, studies show that large-scale environmental degradation is occurring. This is particularly true when fallow periods are shortened to 4 or 5 years. Natural forests over 50 years of age are rare and usually exist only as sacred forest reserves.

Because of erosion and other problems, vast areas are effected. These ecosystems are headwaters for all major river drainages of the country. Floods, deposition of silt, and even changes in the climate itself are all consequences of continuing the practice of Jhum. We can see in this example classic environmental implications. Socially, economically, and politically when the problems are viewed locally, it is difficult to change life styles. However, the problems have far-reaching implications beyond the local scene. As demonstrated in the case of the East Indian practice of Jhum, the accumulation of scientific knowledge alone does not alter public policy including land management practices. The establishment of policy is in itself a complex subject. Henry W. DeBruin, the only land manager present at the conference, presented a paper written by David W. Dahl, Ernest V. Andersen, Trenton Crow, and Steve Pyne, all of the USDA Forest Service, Washington, D.C. This paper, "Fire and Public Policy," compared the 1978 revised Forest Service policy on suppressing forest fires with previous policy--the-so-called 10 a.m. policy. Previous policy, which dated back to 1935, required an aggressive stance that called for sufficient forces on all fires to bring a fire under control by 10 a.m. the following day. This policy stressed an aggressive initial attack and vigorous pursuit of control at the earliest possible time.

Now, Forest Service land managers are being directed to make a situation analysis that includes "cost effective" fire suppression and to allow certain fires to meet specific land management objectives. The new policy specifies that (1) fire management be integrated into land management planning processes, (2) fire suppression may be modified to meet specific land management objectives, (3) land managers are to make use of "prescription fires" to protect, maintain, and enhance natural resource values, and (4) fire protection and use are to be cost effective but also should provide for protection for life and property, public safety, values, and natural resource management programs.

The Forest Service paper examined some factors that contributed to developing public policy relating to fire. Fire Management Policy is presented as a complex, ever-changing reflection of economic forces, social values, cultural mores, political forces, laws, regulations, scientific technology, and philosophy. A history of events and relationships are discussed as they are perceived to be for the example of the U.S. Department of Agriculture, Forest Service Fire Management Policy.

Early challenges to aggressive and all-inclusive fire control policies involved use of fire in southern pine forests and in ponderosa pine in the Southwest. In these ecosystems low-intensity, frequent ground fires were used to control unwanted vegetation. Later, in the 1960's, National Park policy was modified in recognition of the role of fire in maintaining natural ecosystems. Policy on National Forests was modified in the early 1970's to permit use of natural fires in wilderness areas. Although ecological considerations were paramount in the decisions to use fire to maintain natural ecosystems, the most recent significant changes in Forest Service policy were triggered by economic concerns (Gale 1977). Strict adherence to all-out initial attack is expensive with today's rising costs. Trading acres for dollars makes good sense if predictions of fire behavior are valid.

As early as 1971 the Forest Service internally recognized that a broader approach to fire control was needed. In 1972 the term *fire control* was changed to *fire management* and the use of "natural role of fire" was permitted (by exception). This meant that prescribed burning and allowing wildfires to burn under predetermined conditions could accomplish specific objectives.

Escalation of fire expenditures in the 1970's prompted the Office of Management and Budget to request information concerning these rising expenditures. These questions prompted an internal analysis on the efficacy of fire management expenditures (Gale 1977). Conclusions of the report included the determination that existing laws permitted a revision of policy.

Recommendations of the report were:

1. To develop new policies that provide for a more positive approach to fire, consider economics, and encourage line officers to participate in fire management decisions.
2. To establish evaluation procedures for establishing levels of fire management activities and assessing accomplishment.
3. To develop new fire management planning procedures whereby fire planning is conducted within a total land management context, i.e., that fire management is oriented to resource management objectives.
4. To develop accounting and budgeting systems for fire suppression.
5. To develop an evaluation system which includes effectiveness as well as efficiency and that the system be related to total Forest Service programs.

Subsequently, the agency has revised the policy (in 1978) and has taken steps to implement the new policy. It is much to the credit of the Forest Service that such actions and commitments have been positive. Much of the influences addressed in DeBruin's presentation have been involved, although the authors overlooked a critical triggering mechanism in the final stages of a significant shift in the Agency's fire management policy. Although triggered from outside of the Agency, professionalism from within led to a candid and responsible analysis and positive, constructive reaction to the outside stimulus. I feel that this analysis, revision of policy, and implementation of policy is commendable and significant.

The papers presented here have each contributed to our understanding of how principles of fire ecology interact with the realities of land management. There are several reasons that make this an exciting era to be involved in fire management. First, there are the complexities of managing land in today's world. Yesterday's ranger had his problems, e.g., establishing authority in the land of the free. However, the world of today's manager is infinitely more complex; the voice of the public gives conflicting objections, management involves increasing costs, and the pressure to predict the consequences of alternative actions is becoming greater. Thus, judgments must be made which involve a complexity of concerns and over long periods of time while still maintaining environmental quality.

Secondly, policies and administrative procedures have been changed to permit a more objective approach to managing fire. The top management of the USDA Forest Service has established that fire management should be implemented.

Third, we now have the technology and experience in fire suppression and fire use that provides powerful tools of management. Many ingredients are present to make exciting things happen. What we lack is long-standing experience in the application of new knowledge and perspectives. We must proceed with both deliberation and caution, knowing full well that we will make mistakes.

Having been given the opportunity to prove that applying ecological principles will benefit society, greater and greater demands will be placed upon scientists to come up with answers and analytical tools to predict consequences of management alternatives. It will also involve some risk to land managers.

We now need definitive answers on the effects of fire frequency and intensity on ecosystem properties. Both pure and applied research will of necessity become more quantitative and will involve more predictive modeling approaches within a multidisciplinary framework. It will call for better interaction between managers and scientists--more professionalism in all quarters. Given the opportunity and means, land management should be profoundly affected in the coming years. Meanwhile, there is much work to do on the part of both scientists and managers.

James E. Lotan

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Participants in the conference: Row 1--R. Carpenter, W. Robertson, A. Tiedemann, F. Swanson, W. Reiners, N. Christensen; Row 2--A. Qureshi, B. Abeywickrama, S. Sukwong, H. Bormann, G. Wahlgren, M. Heinselman, D. Mueller-Dombois, H. Wright; Row 3--H. Mooney, R. Woodmansee, M. Numata; Row 4--C. Gimmingham, J. Smith, F. Chapin, G. Marten, J. Keeley, S. Keeley, S. Pirages, W. Matthews; Row 5--M. Gill, D. Parsons, P. Windle, P. Ramakrishnan, C. Kucera, I. Noble, B. Kilgore; Row 6--J. Lotan, H. DeBruin, P. Rundel, W. Niering, R. Bonnicksen, L. MacDonald, J. Olson.

